JOURNAL OF AGRICULTURAL RESEARCH

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VOLUME 43

JULY 1–DECEMBER 15, 1931

ISSUED BY AUTHORITY OF THE SECRETARY OF AGRICULTURE
WITH THE COOPERATION OF THE ASSOCIATION OF
LAND-GRANT COLLEGES AND UNIVERSITIES

UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON : 1932

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Published on the 1st and 15th of each month. This volume will consist of 12 numbers and the Contents and Index.

Subscription price: Domestic, $4.00 a year (two volumes)
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JUL 20 1932
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JOURNAL OF AGRICULTURAL RESEARCH

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ERRATA AND AUTHORS' EMENDATIONS

Page 96, fourteenth line from bottom, "1917" should be "1914"; fourth line from bottom, "(1909–1917)" should be "(1909–1914)."
Page 97, Figure 1, "1917" should be "1914" on all plots.
Page 99, Table 1; p. 102, Table 2; p. 107, Table 3; and p. 113, Table 10; footnote *a*, "O, no treatment since 1917" should be "O, no treatment since 1914."
Page 232, second line from bottom, references to Student should be (*1*, *2*, *2a*).
Page 259, Literature Cited, insert (2a) ANONYMOUS.

1923. ON TESTING VARIETIES IN CEREALS.
By Student. Biometrika 15: [271]–293, illus.

Page 267, footnote 4, "14–16" should be "914–916."
Page 285, reference (12), "Sigmonose" should be "Stigmonose."
Page 342, ninth line from bottom, "Figure 6" should be "Figure 7."
Page 371, ninth line from bottom, "U-shaped" should be "V-shaped."
Page 446, sixteenth line from bottom, "notauli" should be "parapsidal furrows."
Page 496, eighteenth line from bottom, "D_1C" should be "D_1c."
Page 615, Table 3, under "Dilution," line 21, "1–2,500" should be "1–2,400"; line 22, "1–2,400" should be "1–2,800."
Page 639, twenty-third line from bottom, "104" ahould be "1.04."
Page 649, heading of Table 7, omit "and" between "dates" and "on."
Vol. 43, No. 8, Table of Contents, fifth article, and on page 715, "Humfeldt" should be "Humfeld."
Page 814, line 11, "50°" should be "60°."
Page 818, fourth line from bottom, "(p. 865)" should be "(p. 815)."
Page 836, citation (1), "26 p." should be "36 p."
Page 895, line 16, "isolation" should be "isolations."
Page 903, Literature Cited, fourth reference, "Châtigier" should be "Châtaignier."
Page 963, Table 1. In the frequency distribution for "Rowden 3003, W," no frequencies occur in classes 33.1–34, 34.1–35, and 35.1–36.
Page 1057, legend for Figure 1, third line, omit "no count or dosage on" between "and" and "August."

JOURNAL OF AGRICULTURAL RESEARCH

VOL. 43 WASHINGTON, D. C., JULY 1, 1931 NO. 1

THE USE OF POLYMORPHIC CURVES IN DETERMINING SITE QUALITY IN YOUNG RED PINE PLANTATIONS [1]

By HENRY BULL

Formerly Assistant Forester, Forestry Department, Connecticut (New Haven) Agricultural Experiment Station [2]

INTRODUCTION

In the summer of 1928 the forestry and soils departments of the Connecticut Agricultural Experiment Station began an investigation of the relation of soil conditions to the growth of planted red pine (*Pinus resinosa*), which constituted part of a more general research project relating to the effect of soil conditions on the composition and rate of growth of the forest. A progress report covering all phases of this project will be published later as a bulletin of the station. As a result of the experience gained in the earlier studies it seemed desirable to concentrate, temporarily at least, upon a single tree species that could be found growing in pure or nearly pure stands over a wide range of soil and site conditions. In order to make valid comparisons possible such a species should be developing under virtually the same conditions of density, competition, treatment or lack of treatment. Also, it should be free from serious attacks by insect or fungous enemies.

Planted red pine, spaced about 6 by 6 feet and developing without interference by hardwoods, is the only species in Connecticut that fulfills such specifications, and it was therefore selected. Red pine has been and still is a deservedly popular species for forest planting in this State, there being some 5,000 acres now (1929) successfully planted. A majority of the plantations have been made on lands formerly tilled or pastured. White pine would have been an equally good species to use in this study but for the prevalence of deformed stems caused by the white pine weevil, which makes it impossible to secure either comparable or representative height measurements.

A study of the correlation between the growth of red pine and soil conditions required the accurate determination of the site quality at a number of selected stations or plots. This paper, describing the development, testing, and use of accurate methods for the determination of site quality in red pine plantations, is offered in the belief that it may be of value and interest to foresters, especially those dealing

[1] Received for publication Dec. 8, 1930; issued July, 1931.

[2] The author wishes to acknowledge the valuable assistance of the following foresters who read and commented upon the manuscript at various stages of its preparation and who offered constructive suggestions: Henry W. Hicock, assistant forester, and W. O. Filley, forester, of the Connecticut Agricultural Experiment Station; C. Edward Behre, director, Northeastern Forest Experiment Station; Profs. R. C. Hawley and H. H. Chapman of the Yale School of Forestry; and Donald Bruce of the branch of research, U. S. Forest Service. Of these, the advice and comments of Henry W. Hicock, with whom the author worked and who was largely responsible for the initiation and completion of the red pine study, were especially valuable.

with similar problems. The findings concerning the relative merits of anamorphic and polymorphic site-quality curves are applicable far beyond the narrow limits of red pine plantations and indicate the need of further research along similar lines.

After many years of controversy and suggestions concerning the measurement of site quality, during which time a majority of foresters declared themselves in favor of the height attained by dominant trees, a committee of the Society of American Foresters recommended that this be the standard for determining site quality for the construction and application of yield tables (*5*).[3] In this study, therefore, height growth of dominant trees has been used as the criterion of site quality.

All the data were secured in Connecticut, but there seems to be no reason why the following tables and figures should not also apply to other red pine plantations (at least to those in the Northeast) established and growing under the same conditions. There may, however, be both better and poorer sites than any found in Connecticut. Unfortunately, there were not data for plantations more than 31 years old. The great majority of the plantations studied were 17 or 18 years old.

FIELD WORK—SECURING THE DATA

During the field season of 1928, nearly all the red pine plantations in Connecticut in which the trees had attained an age of at least 10 years (including age of planting stock) were visited, and one or more stations at which to collect data were selected in each. The selected stations were called temporary plots. The soil at each plot was described and sampled (for laboratory study) either when the trees were measured or subsequently. In the latter case, the plots were accurately located on a map and marked or tagged so that the exact locations might be revisited.

The total heights of dominant trees at the end of the 1928 growing season, and also the total heights at different years in the past, were measured at each plot. No other measurements of the trees were taken. While the classification of crowns is a matter of personal judgment, it is felt that the trees selected for measurement at each plot fairly represent the dominant stand at that particular location.

Great care was taken in choosing the stations or plots. They were selected only where the planted trees had been entirely free at all times from hardwood competition and where the spacing was approximately 6 by 6 feet. Every effort was made to establish stations only where all growing conditions except those due to purely edaphic factors were uniform. Stations were selected over as wide a range of soil and growth conditions as possible.

Heights were measured with a graduated pole to the nearest tenth foot. At least 10 dominant trees were measured at each station. Where there was an unusually wide range of dominant heights (about 3 feet or more at 17 and 18 years) more than 10 trees were measured. No hard and fast mathematical rule was used in determining how many heights to measure at any given station. At each one, however, there were enough height measurements made (in the judgment of the field worker after an inspection of the first 10 height values) to give an average that fairly represented the dominant crown class. The cor-

[3] Reference is made by number (italic) to Literature Cited, p. 28.

rectness of such judgment was checked from time to time by measuring from 6 to 10 extra heights on a plot where a supposedly adequate number of heights had already been measured, and then comparing the average of the original group of heights with the average of that group plus the extra heights. The two averages were very rarely more than 0.3 foot apart. To express mathematically the reliability of the average dominant height value secured at each plot, the standard error was computed. For every such height value the standard error was under ± 0.4 foot, and for about 99 per cent of the values it was under ± 0.3 foot.

SITE INDEX—THE MEASURE OF SITE QUALITY

As stated, the use of height growth as an indicator of site is very widely accepted and has been advocated as a standard practice. The measure of site quality on this basis is site index, the total height attained by the average dominant tree in an even-aged stand at an arbitrarily selected standard or classification age. This age has been set at either 50 or 100 years, depending largely on the age of maturity of the species, in most of the studies of site quality made by the United States Forest Service. In this study, however, a classification age of only 15 years has been used, this being approximately the average of all ages tallied in taking height-age measurements. For example, a 15-year-old plantation in which the average dominant trees are 18 feet high has a site index of 18 feet. In the case of plantations younger or older than 15 years, the site-index figure represents the average dominant height that these plantations will have or did have at 15 years. Plantations of all ages are thus adjusted to the common basis of average dominant height at 15 years.

The use of 15 years *since planting* rather than 15 years *total age* was given consideration because a classification age representing a period since planting would in many ways be more practical to use than one which consists of age of planting stock plus period since planting. It was found, however, that a site-index table based on a period since planting could be made to serve accurately for only one given age of stock. Hence, although four different tables might have been prepared (for 2, 3, 4, and 5 year old planting stock, respectively), it was much simpler to make one table based on total age, since in either case an accurate determination of site index depends not only upon knowledge of the period since planting but of the age of the stock used as well; that is, the actual total number of years from seed. The total age for the plantations studied was taken from office records.

ANAMORPHIC VERSUS POLYMORPHIC SITE INDEX CURVES

By use of a set of curves after the method of Bruce (*2*) or by the use of a nomogram after the method of Reineke (*6*), any average dominant height at any age is readily converted into site index. Both Bruce and Reineke use anamorphosis in preparing their respective curves and nomograms. That is, a single graduating curve is drawn from the paired height-age values secured at as many different sites as possible, and from this curve—representing the average progress of height with age—a curve for each site index is drawn proportional to the graduating curve and spaced proportionally from its neighbors. As a result of anamorphosis, therefore, the curve of

the poorest site sidex has exactly the same characteristics as the curve of all other site indices. If the period of maximum height growth is from 10 to 20 years on the graduating curve, the period of maximum height growth will also be from 10 to 20 years on all the other curves.

Bruce's anamorphic method was applied to the height-age data as the first step in this study. The graduating or basis curve was based on paired height-age values secured at 168 plots covering the entire range of site quality. A set of anamorphic site-index curves (fig. 1) was drawn from this graduating curve. There appears to be nothing in the literature to show whether or not anamorphosis is applicable to red pine, but it has given satisfactory results with other species when used in the preparation of yield tables where a very high degree of accuracy in the determination of individual site indices is not required.

Careful study of the actual progress of height growth on various sites, particularly the poorest and the best, showed, however, that the anamorphic curves were not applicable, since the curves for the poorest sites do not have the same characteristics as the curves for the best sites.

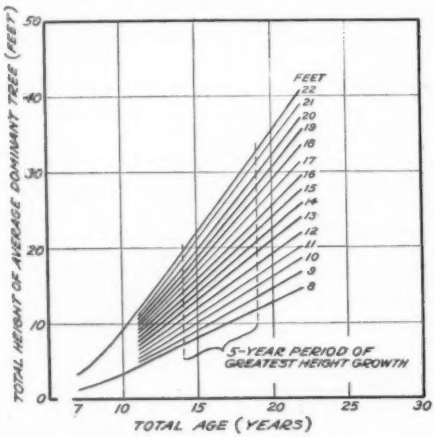

FIGURE 1.—Anamorphic site-index curves for red pine. (Classification age: 15 years)

In Figure 2, the so-called polymorphic curve representing a site index of 21 feet is an actual average (i. e., as far as 18 years; the remainder is adapted from the set of polymorphic curves made at a later date) secured from 10 of the best sites encountered in this study. The polymorphic curve representing a site index of 8.5 feet is an actual average of the three poorest sites. For the purpose of comparison, the two anamorphic curves from Figure 1 having the same site indices are shown in broken lines. As will shortly be explained, the set of site-index curves finally constructed for use in place of the set of anamorphic site-index curves was made from several graduating curves, hence the individual curves in the set have as many different forms and the term "polymorphic" serves both to describe the new curves and to distinguish them from anamorphic curves. The so-called polymorphic curves of Figure 2 were constructed from the actual data obtained at a few good and poor sites, with the exception of the 18–31 year portion of the upper curve, as just stated, and were therefore obviously not taken from the complete set of polymorphic curves—which at that time were not in existence. The point is that to all intents and purposes they might have been taken from such a set, are in fact the partial basis for the uppermost and lowermost members of such a set, and the term "polymorphic" is therefore entirely applicable.

It will be noted that the actual progress of height growth has not the same characteristics on these two extreme sites, although according to the anamorphic curves the characteristics of the two progressions

are identical. On the poorest sites height growth proceeds very slowly at first, gradually increasing to a maximum rate in the five years between the ages of 20 and 25 years. There is then a slight decrease, values beyond 31 years being unavailable. On the best sites height growth proceeds very rapidly from the start, reaching its

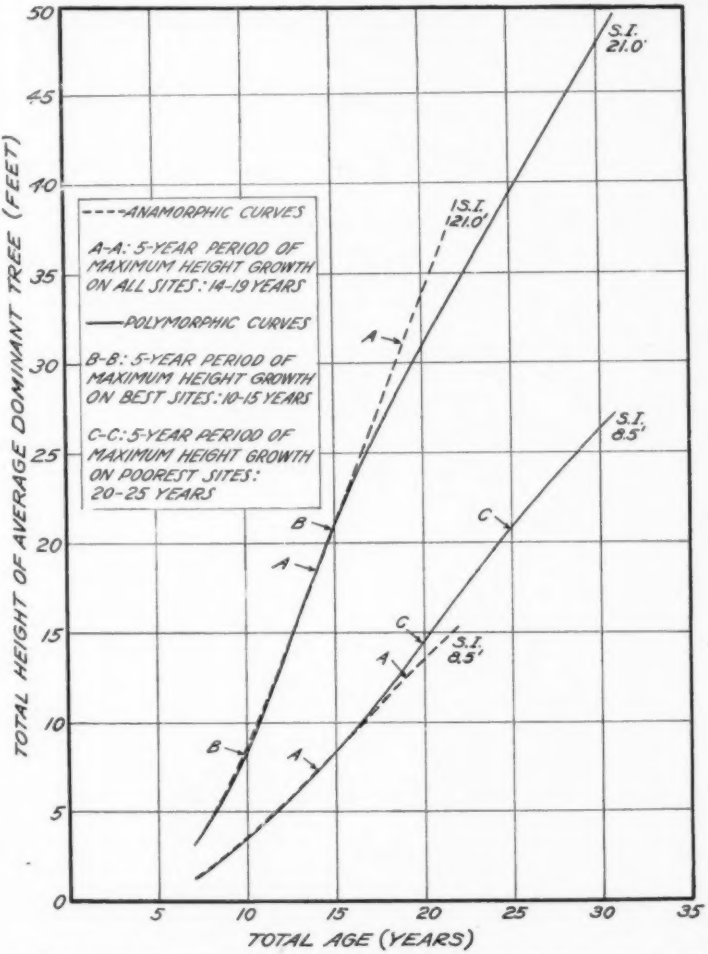

FIGURE 2.—Comparison of anamorphic site-index curves with polymorphic site-index curves. (Classification age: 15 years)

maximum rate in the five years between the ages of 10 and 15 years, and then decreasing sharply. In reality, then, the curves of the two extreme sites are much closer to each other beyond 15 years than anamorphic curves would indicate, and probably a very limited range of intermediate sites actually show the 5-year period of maximum height growth between the ages of 14 and 19 years as in the case of

the anamorphic curves. At 14 years the 5-year period of maximum height growth is very nearly over on the best sites, whereas at 19 years this period has not yet begun on the poorest sites.

Since a high degree of accuracy in the determination of site quality is essential to a study of the correlation between site quality and site factors, the anamorphic method was discarded as unsuitable. If it had been required to determine site index only to the nearest 10-foot class at 50 years, corresponding to about 3 feet at 15 years for red pine, the anamorphic curves might have been satisfactory. It should be noted in Figure 2, however, that the farther the anamorphic curves are projected (i. e., the greater the age) the greater is the error incurred through their use.

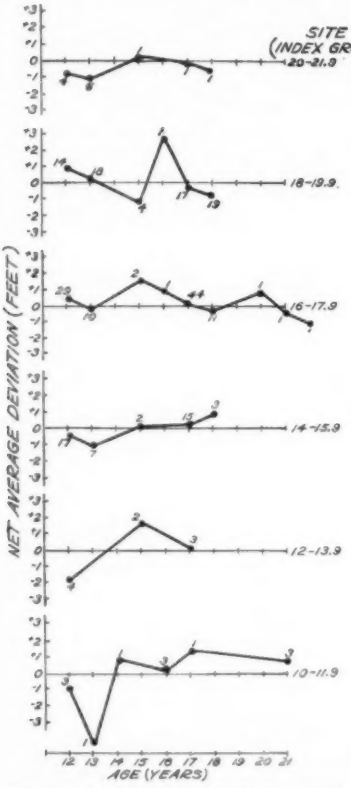

FIGURE 3.—Net average deviations of site-index values calculated from anamorphic curves. (Data from Table 1)

It was entirely for the purpose of showing this increase in error with increase in age that the 18–31 year portion of the upper polymorphic curve was added to the original Figure 2 before reproduction in this paper. The added portion was not based on actual data but on the trend exhibited in the completed set of polymorphic curves (fig. 4) which will shortly be discussed. Note that even though the form of the single graduating curve for the anamorphic system were altered—thus changing the form of all the individual curves—(and either the upper or the lower anamorphic curve shown in Figure 2 were thus made to duplicate the corresponding polymorphic curve) the other anamorphic curve would be even more divergent from the other polymorphic curve than it is at present. A change in the form of one anamorphic curve necessarily means a similar change in the same direction in the form of all other anamorphic curves in the set. The anamorphic curves by their very nature can not possibly show the actual progress of height with age in this particular case. The error increases with age and will either be of about the same magnitude for the good sites and the poor sites or smaller for one group at the expense of being larger for the other group.

Figure 3 and Table 1 also show the inadequacy of the anamorphic curves for the accurate determination of site index. A few words of explanation about the deviations shown in the figure and in the tables

will be necessary before this can be appreciated. For each of the plots at which the height 5 years ago was obtained, and for each of the plots at which heights 5 and also 10 years ago were obtained (in addition to the present height), it was possible to determine two and three site indices, respectively. In theory, these two or three site-index values should be identical. Actually, they are very rarely identical. This is because few individual plots maintain a height growth in exact accordance, year after year, with site-index curves representing average trends secured from a large number of plots. The deviations of the tables (shown graphically and in a slightly different arrangement in fig. 3) are the differences between site-index values determined for the same plot at ages spaced 5 years apart. The deviation resulting from the older age being associated with the greater site index was called a plus deviation. When the older age was associated with the lesser site index, the resultant deviation was given a minus sign. The age by which the deviations were classified (Table 1) was the older of the two ages at which site-index values were compared. The site-index group by which the deviations were classified (Table 1) was the one in which occurred the site-index value associated with the older age.

TABLE 1.—*Deviations of site-index values at ages spaced five years apart, calculated from anamorphic curves* [a]

CLASSIFIED BY AGE

Age [b] (years)	Deviations					
	Plus	0	Minus	Sum	Total	Average
	Number	*Number*	*Number*		*Number*	
12	35	1	35	106.5	71	±1.50
13	17	2	23	54.6	42	±1.30
14	1			.9	1	±.90
15	5	1	5	12.4	11	±1.13
16	3	1	1	4.4	5	±.88
17	38	3	37	44.6	78	±.57
18	8	1	25	32.2	34	±.95
19						
20	1			.8	1	±.80
21	3		1	2.4	4	±.60
22			1	1.2	1	±1.20
Total	[c] 111	[d] 9	[e] 128	260.0	248	±1.05

CLASSIFIED BY SITE INDEX

Site-index group [f]	Deviations					
	Plus	0	Minus	Sum	Total	Average
	Number	*Number*	*Number*		*Number*	
10 to 11.9	7	1	4	13.0	12	±1.08
12 to 13.9	4		5	14.7	9	±1.63
14 to 15.9	19	2	23	51.1	44	±1.16
16 to 17.9	52	3	42	100.2	97	±1.03
18 to 19.9	27	3	43	69.6	73	±.95
20 to 21.9	2		11	11.4	13	±.88
Total	[c] 111	[d] 9	[e] 128	260.0	248	±1.05

[a] The 128 plots, furnishing 248 comparisons or deviations, that were used for this test were also used for the test reported in Table 4.
[b] The higher age of the two at which the site indices are compared.
[c] 44.8 per cent.
[d] 3.6 per cent.
[e] 51.6 per cent.
[f] The group in which occurs the site index associated with the older age of the two at which site indices are compared.

An example may make this clearer. For a certain 18-year-old plot we have the following height-age data: 18 years, 23.1 feet (average dominant height); 13 years, 13.2 feet; 8 years, 3.5 feet. The corresponding site-index values, from a table read from Figure 1, are 17 feet, 17.4 feet, and 16 feet, respectively. The deviations for this plot that would be entered in Table 1 would then be: At 18 years, a deviation of −0.4 foot; at 13 years, a deviation of +1.4 feet. In Table 1 would also be entered, from the same plot: For site-index groups 16–17.9, deviations of −0.4 foot and +1.4 feet, respectively. Table 1 contains summaries derived from such individual deviations.

On the whole, the plus and minus deviations seem to balance one another well enough, but there is nevertheless a definite tendency for the deviations of the older plots (16 years and over) of the higher indices to be preponderantly minus and the deviations of the older plots of the lower indices to be preponderantly plus. (Fig. 3.) This is equivalent to stating as above that with increase in age the curves of the best and the poorest sites, instead of getting farther and farther apart as represented by the anamorphic curves, are much more nearly parallel. The same tendency is readily discernible in Table 1.

The data are admittedly very weak beyond 18 years and, as may be seen in Figure 2, there is no consistent divergence between anamorphic curves and those accurately depicting the development of height growth until 15 years is reached. From 15 to 18 years is only a very small section on which to base conclusions, and at 18 years the divergence is not yet very great. In Figure 3 and Table 1, therefore, the poor fit of the anamorphic curves to the data does not stand out very strongly because of the extreme weakness of the data beyond the 18-year mark. The figure and table are, nevertheless, given here because they show the misfit of the anamorphic curves to the data in a different and much more detailed, if less striking, manner than does Figure 2. In examining them, and later in comparing them with the corresponding figure and tables based on polymorphic curves, small differences in trend must be noted and appreciated and large differences must not be expected, the data being of such a nature as to permit of no other treatment.

Before passing on to the development of a set of curves to replace the anamorphic curves it should be stated that Bruce has at all times been full cognizant of the possible errors incurred through the use of the anamorphic method. In an early article (*1, page 782*), he says:

> In appraising this method, its dangers and the objections to its use should be as clearly recognized as its advantages. Like all things of value it may be misused and poor results may be secured with it. The chief danger, of course, is that of using it in cases to which it is not properly applicable. If this is done the curves will be forced into a false shape. Constant alertness is necessary to recognize this condition when it occurs so that the method may be abandoned. The danger sign is not so much a failure of the points on the curves to fall into a linear zone when anamorphosed as some regularity in their manner of departing from this form. Experience, too, is often a guide. In the case, for example, of yield table curves of volume over age by site classes the use of this method will so completely harmonize the curves that the age of culmination of current annual growth and of mean annual growth will be the same for all sites. As this is contrary to experience, the method should be used in such cases only where the data is too weak to permit any determination of the differences in these ages due to site quality.

As we have seen, anamorphic site-index curves for red pine are open to very nearly the same objections cited by Bruce. In a later section it will be shown that several other coniferous species are similar to red pine in respect to the fact that anamorphosis produces site-index curves that do not accurately portray the actual development.

POLYMORPHIC SITE-INDEX CURVES—THEIR CONSTRUCTION AND CHARACTERISTICS

Twelve of the 168 plots were rejected because of extremely abnormal and irregular progression of height growth, and the remaining 156 plots were divided into 7 site-quality groups, each with an approximate range of 2 feet of site index. Since it was desired to place within a given group only those plots that were really of the same site quality, growth during a 5-year period (between 7 and 12, and between 8 and 13 years in most cases) just before the stand closed was used as the basis, in the belief that it was a more accurate criterion of site quality than site-index values derived from looking up total heights and total ages on the anamorphic curves. In this way the entire range of site index (corresponding to a range of 8 to 22 feet on the anamorphic curves) was included in the seven groups.

Seven graduating curves were then constructed—each based on the height-age data from all the plots within a single group. The number of plots and the number of height-age coordinates for each site-quality group are shown in Table 2.

TABLE 2.—*Basic data used in constructing polymorphic site-index curves*

Group No.	Approximate range in site index at 15 years	Sample plots	Points upon which to base a curve	Group No.	Approximate range in site index at 15 years	Sample plots	Points upon which to base a curve
	Feet	*Number*	*Number*		*Feet*	*Number*	*Number*
1	8–10	5	23	6	18–20	52	238
2	10–12	5	12	7	20–22	11	57
3	12–14	7	18				
4	14–16	29	95	Total		156	643
5	16–18	47	200				

Now, instead of there being only one graduating curve based on all plots from the poorest site index (8 feet) to the best (22 feet) there were seven graduating curves, each based on a definite portion of the total range. Each of the seven graduating curves was then made the basis for a small group of anamorphic curves, ranging from 1 to 2 feet on either side of their graduating curve and passing through even-foot marks at 15 years. Next, the seven groups of anamorphic curves were plotted together in a single graph. The anamorphic curve coinciding with or within 1 foot of the graduating curve from which it was constructed was considered a final site-index curve, and each remaining final curve (for even 1-foot intervals at 15 years) was drawn by means of weighted averaging of the anamorphic curves on either side of each even-foot mark not already accounted for. For example, the final curve for a site index of 14 feet was the 14-foot anamorphic curve from the Group 3 graduating curve (which passed through 13.8 feet). The final curve for a site index of 16 feet was the 16-foot anamorphic curve from the Group 4 graduating curve (which

passed through 15.6 feet). The final curve for a site index of 15 feet was constructed by averaging the two anamorphic curves from Groups 3 and 4 that passed nearest the 15-foot mark. Slightly greater weight was given the curve of Group 4 than the curve of Group 3.

The complete set of site-index curves constructed in this way is shown in Figure 4. Table 3 was read off from this figure. Although anamorphosis was used within each separate group to make several curves similar in shape to the graduating curve for that group, the final curves, far from representing an anamorphic series having one basic form, are of several (seven) different forms and therefore may be called "polymorphic" curves.

The annual height increment between 7 and 31 years of age for all sites is shown in Table 4, the values for which were read from Table 3. It will be noted that with increase in site index there is a steady decrease in the age that fixes the beginning of the 5-year period of maximum height growth. This period is shown also in Figure 4, where it is apparent that for all sites of 12 feet or better this period begins when the dominant stand averages 9 feet in height (ranging from 8 to 10.5 feet), whereas for all sites of 11 feet or less this period begins when the dominant stand averages between 12 and 13 feet in height (ranging from 11.8 to 12.8 feet). The age at which maximum height increment begins thus appears to be governed by the height of the dominant stand and by the site quality. It will be remembered that on the anamorphic curves (fig. 1) the 5-year period of maximum height growth begins at 14 years and ends at 19 years for all sites.

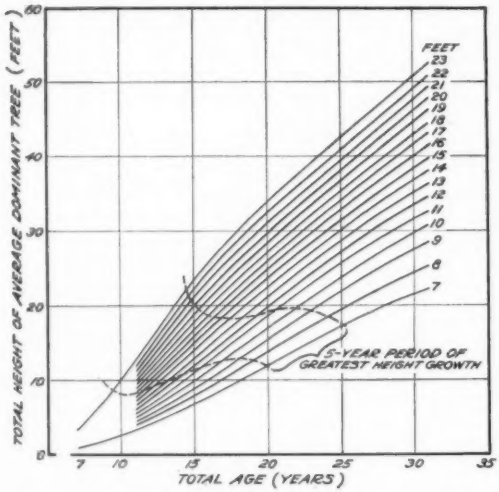

FIGURE 4.—Polymorphic site-index curves for red pine. (Classification age: 15 years)

When site-index curves are anamorphic a constant and exact relationship exists between any two site indices and the respective heights attained at any given age. For example, if the height at 30 years is x feet for a site index of 10 feet, the height at 30 years will necessarily be $2x$ feet for a site index of 20 feet. No such constant and exact relationship exists between polymorphic curves. This is no disadvantage of polymorphic curves, however, and in at least one respect may be an advantage. The constant and exact relationship between anamorphic curves is entirely a relationship of height. There is absolutely no such relationship between site index and yield, the truest and most valuable basis for making distinctions between

TABLE 3.—*Site-index table for planted red pine, based on polymorphic curves*[a]

Site index	Total height of average dominant tree in feet at total age in years indicated																								
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
7	0.9	1.4	2.1	2.8	3.5	4.3	5.2	6.1	7.0	7.9	8.8	9.7	10.7	11.7	12.8	13.9	15.0	16.1	17.2	18.2	19.2	20.0	20.8	21.6	22.3
8	1.1	1.6	2.4	3.2	4.0	4.9	5.9	6.9	8.0	9.0	10.1	11.2	12.4	13.6	14.8	16.0	17.2	18.4	19.6	20.8	21.9	23.0	23.9	24.8	25.6
9	1.3	1.9	2.7	3.6	4.5	5.5	6.6	7.8	9.0	10.2	11.4	12.6	13.9	15.2	16.5	17.9	19.3	20.6	21.9	23.2	24.5	25.6	26.7	27.7	28.6
10	1.4	2.2	3.0	4.0	5.0	6.1	7.4	8.7	10.0	11.3	12.7	14.1	15.5	16.9	18.3	19.7	21.1	22.5	23.9	25.2	26.5	27.8	28.9	30.0	30.9
11	1.6	2.4	3.3	4.4	5.5	6.7	8.1	9.5	11.0	12.5	14.0	15.5	17.0	18.5	20.0	21.4	22.8	24.2	25.6	27.0	28.3	29.6	30.8	31.9	32.9
12	1.8	2.6	3.6	4.8	6.0	7.3	8.8	10.4	12.0	13.6	15.2	16.8	18.4	19.9	21.4	22.9	24.4	25.8	27.2	28.6	30.0	31.3	32.6	33.8	34.9
13	2.0	2.8	3.9	5.2	6.5	7.9	9.5	11.2	13.0	14.7	16.4	18.0	19.7	21.3	22.8	24.3	25.8	27.3	28.7	30.1	31.5	32.9	34.2	35.4	36.5
14	2.1	3.0	4.2	5.6	7.0	8.6	10.3	12.1	14.0	15.8	17.5	19.2	20.9	22.5	24.1	25.7	27.3	28.8	30.2	31.6	33.0	34.4	35.8	37.1	38.3
15	2.3	3.2	4.5	5.9	7.5	9.3	11.1	13.0	15.0	16.8	18.6	20.3	22.0	23.7	25.3	26.9	28.5	30.0	31.5	33.0	34.5	36.0	37.4	38.8	40.1
16	2.4	3.4	4.7	6.3	8.0	9.9	11.9	13.9	16.0	17.9	19.7	21.4	23.1	24.8	26.4	28.0	29.6	31.2	32.8	34.4	36.0	37.5	39.0	40.4	41.8
17	2.6	3.6	5.0	6.7	8.5	10.5	12.7	14.9	17.0	18.9	20.7	22.4	24.1	25.8	27.4	29.1	30.7	32.4	34.0	35.7	37.3	38.9	40.5	42.0	43.4
18	2.8	3.8	5.3	7.1	9.1	11.2	13.5	15.8	18.0	19.9	21.7	23.4	25.2	26.9	28.6	30.3	32.0	33.7	35.4	37.1	38.8	40.4	42.0	43.5	44.9
19	2.9	4.1	5.6	7.5	9.6	11.9	14.3	16.7	19.0	21.0	22.8	24.6	26.4	28.1	29.8	31.5	33.2	34.9	36.6	38.3	40.0	41.7	43.4	45.0	46.5
20	3.0	4.3	6.0	8.0	10.2	12.6	15.1	17.6	20.0	22.1	24.0	25.8	27.6	29.3	31.1	32.8	34.6	36.3	38.0	39.7	41.4	43.1	44.8	46.4	47.9
21	3.2	4.5	6.3	8.4	10.8	13.3	16.0	18.6	21.0	23.2	25.2	27.0	28.8	30.6	32.4	34.1	35.9	37.6	39.4	41.1	42.8	44.5	46.2	47.8	49.4
22	3.4	4.8	6.6	8.8	11.4	14.1	16.8	19.5	22.0	24.3	26.4	28.3	30.1	31.9	33.7	35.5	37.3	39.1	40.9	42.6	44.3	46.0	47.7	49.3	50.9
23	3.5	5.0	7.0	9.3	12.0	14.9	17.7	20.4	23.0	25.4	27.6	29.6	31.5	33.3	35.1	36.9	38.7	40.5	42.3	44.1	45.8	47.5	49.2	50.9	52.5

[a] Classification age, 15 years. The block inclosed by a heavy black line contains probable values. There were no data for this section. A glance at Fig. 4 will show that these values can hardly be very much in error.

TABLE 4.—*The annual height increment of planted red pine, based on polymorphic curves* [a]

Increase in total height in feet of average dominant tree for total ages indicated (fixing a 1-year period)

Site index	7 to 8	8 to 9	9 to 10	10 to 11	11 to 12	12 to 13	13 to 14	14 to 15	15 to 16	16 to 17	17 to 18	18 to 19	19 to 20	20 to 21	21 to 22	22 to 23	23 to 24	24 to 25	25 to 26	26 to 27	27 to 28	28 to 29	29 to 30	30 to 31
7	0.5	0.7	0.7	0.7	0.8	0.9	0.9	0.9	0.9	0.9	0.9	1.0	1.0	1.1	1.1	1.1	1.1	1.1	1.0	1.0	0.8	0.8	0.8	0.7
8	.5	.8	.8	.8	.9	1.0	1.0	1.1	1.0	1.1	1.1	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.1	1.1	.9	.9	.8
9	.6	.8	.9	.9	1.0	1.1	1.2	1.2	1.2	1.2	1.2	1.3	1.3	1.3	1.4	1.4	1.3	1.3	1.3	1.3	1.1	1.1	1.0	.9
10	.8	.8	1.0	1.0	1.1	1.3	1.3	1.3	1.3	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.3	1.3	1.3	1.1	1.1	.9
11	.8	.9	1.1	1.1	1.2	1.4	1.4	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.4	1.4	1.4	1.4	1.4	1.3	1.3	1.2	1.1	1.0
12	.8	1.0	1.2	1.2	1.3	1.5	1.6	1.6	1.6	1.6	1.6	1.6	1.5	1.5	1.5	1.5	1.4	1.4	1.4	1.4	1.3	1.3	1.2	1.1
13	.8	1.1	1.3	1.3	1.4	1.6	1.7	1.8	1.7	1.7	1.6	1.7	1.6	1.5	1.5	1.5	1.5	1.4	1.4	1.4	1.4	1.3	1.2	1.1
14	.9	1.2	1.4	1.4	1.6	1.7	1.8	1.9	1.8	1.7	1.7	1.7	1.6	1.6	1.6	1.6	1.5	1.4	1.4	1.4	1.4	1.4	1.3	1.2
15	.9	1.3	1.4	1.6	1.8	1.8	1.9	2.0	1.8	1.8	1.7	1.7	1.7	1.6	1.6	1.6	1.5	1.5	1.5	1.5	1.5	1.4	1.4	1.3
16	1.0	1.3	1.6	1.7	1.9	2.0	2.0	2.1	1.9	1.8	1.7	1.7	1.7	1.6	1.6	1.6	1.6	1.6	1.6	1.5	1.5	1.4	1.4	1.3
17	1.0	1.4	1.7	1.8	2.0	2.2	2.2	2.1	1.9	1.8	1.7	1.7	1.7	1.6	1.7	1.6	1.7	1.6	1.6	1.6	1.6	1.5	1.5	1.4
18	1.0	1.5	1.8	2.0	2.1	2.3	2.3	2.2	1.9	1.8	1.7	1.8	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.6	1.6	1.6	1.5	1.4
19	1.2	1.5	1.9	2.1	2.3	2.4	2.4	2.3	2.0	1.8	1.8	1.8	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.6	1.6	1.5	1.4
20	1.3	1.7	2.0	2.2	2.4	2.5	2.5	2.4	2.1	1.9	1.8	1.8	1.7	1.8	1.7	1.8	1.7	1.7	1.7	1.7	1.7	1.7	1.6	1.5
21	1.3	1.8	2.1	2.4	2.5	2.7	2.6	2.4	2.2	2.0	1.8	1.8	1.8	1.8	1.7	1.8	1.7	1.8	1.7	1.7	1.7	1.7	1.6	1.5
22	1.4	1.8	2.2	2.6	2.7	2.7	2.7	2.5	2.3	2.1	1.9	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.7	1.7	1.7	1.7	1.6	1.6
23	1.5	2.0	2.3	2.7	2.9	2.8	2.7	2.6	2.4	2.2	2.0	1.9	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.7	1.7	1.7	1.7	1.6

[a] Classification age: 15 years. Black indicates 5-year period of maximum height growth.

sites. A plot having an anamorphic site index of 20 feet may be thought of as exactly twice as good as a plot having a site index of 10 feet only with respect to height. It may be more than twice, exactly twice, or less than twice as good with respect to yield. This last statement also holds true for a polymorphic site index of 20 feet as compared with one of 10 feet. With either type of site index the exact relationship to yield can be determined only by going to the considerable trouble of making a yield table, and even then the relationship will be found to vary according to variation in age.

Before passing to the next section it should be explained that the method of obtaining height-age data for the construction of polymorphic curves was essentially that of determining height growth in a stem analysis of dominant trees. In the present case, measuring and counting down from the tips of the dominant pines gave a series of height-age values tracing the development of these individuals. Thus height-age data that would be obtained in an ordinary stem analysis of felled trees were obtained on standing trees. It has been customary, however, in American forestry practice to frown upon the use of stem analyses of dominant trees in constructing height-over-age curves for the purpose of site classification because, according to Bruce (*2*) and others, the number of dominant trees varies with age. For various reasons, which need not be elaborated here, this does not appear to the author to be a valid or serious objection, but the present work can not evoke this objection at all, for the very good reason that the plantations dealt with are still so young that the number of dominants has not yet been reduced from the number present when dominance first became expressed. No dominants have yet dropped into a lower crown class.

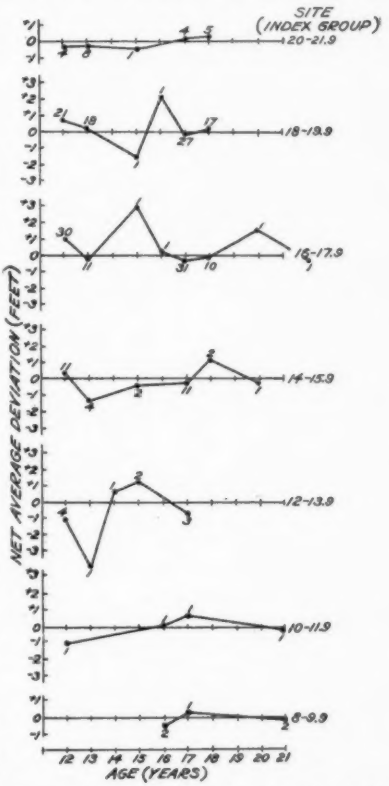

FIGURE 5.—Net average deviations of site-index values calculated from polymorphic curves. (Data from Table 5)

TESTING THE POLYMORPHIC CURVES

The same test that was applied to the anamorphic curves was applied to the polymorphic curves. That is, the plus and minus deviations were computed by age classes and by site-index groups. The results of this test as applied to the same 128 plots already used in testing the anamorphic curves are presented in Table 5 and Figure 5. Comparing these directly with Table 1 and Figure 3, it may be

seen that whereas the total number of plus and minus deviations now balance very little better than before and the average deviation is actually very slightly greater, not a single individual age or site-index class now shows a pronounced deviation on either the plus or minus side.

In Table 1 it is seen that the anamorphic curves produce at 18 years about three times as many minus deviations as plus deviations. At the remaining ages the deviations balance as well as could be expected. In Table 5 it is seen that the polymorphic curves produce equal numbers of plus and minus deviations at 18 years. At the remaining ages the deviations are again well balanced. The very slightly larger average deviation incurred by use of the polymorphic curves is due entirely to the larger deviations at 12 and 13 years, the deviations at 17 and 18 years being less than with the anamorphic curves.

In Table 1 there is a distinct tendency toward a preponderance of minus deviations in the two highest site-index classes, especially in the highest. In Table 5 no such tendency exists, the deviations balancing very well from the poorest to the best site-index classes.

TABLE 5.—*Deviations of site-index values at ages spaced five years apart, calculated from polymorphic curves* [a]

CLASSIFIED BY AGE

Age [b] (years)	Deviations					
	Plus	0	Minus	Sum	Total	Average
	Number	*Number*	*Number*		*Number*	
12	39	2	30	119.2	71	±1.68
13	17	3	22	58.8	42	±1.40
14	1			.8	1	±.80
15	3		8	15.4	11	±1.40
16	3		2	3.4	5	±.68
17	29	6	43	43.1	78	±.55
18	17	0	17	19.6	34	±.58
19						
20	1			1.6	1	±1.60
21	1	2	1	.2	4	±.05
22	1			.2	1	±.20
Total	[c] 112	[d] 13	[e] 123	262.3	248	±1.06

CLASSIFIED BY SITE INDEX

Site-index group [f]	Deviations					
	Plus	0	Minus	Sum	Total	Average
	Number	*Number*	*Number*		*Number*	
8 to 9.9	2	2	1	1.5	5	±0.30
10 to 11.9	2		2	1.8	4	±.46
12 to 13.9	5		6	17.7	11	±1.61
14 to 15.9	13	2	16	35.6	31	±1.15
16 to 17.9	41	5	40	108.4	86	±1.26
18 to 19.9	40		49	82.5	89	±.93
20 to 21.9	9	4	9	14.8	22	±.67
Total	[c] 112	[d] 13	[e] 123	262.3	248	±1.06

[a] The same 128 plots, furnishing 248 comparisons or deviations, were used for this test as for the test reported in Table 1.

[b] The higher age of the two at which the site indices are compared.

[c] 45.2 per cent.

[d] 5.2 per cent.

[e] 49.6 per cent.

[f] The group in which occurs the site index associated with the older age of the two at which site indices are compared.

In Figure 3, as noted in a previous section, the deviations of the older plots of the higher indices are almost entirely minus, whereas the deviations of the older plots of the lower indices are almost entirely plus. This is not true of Figure 5, where the plus and minus deviations are very irregularly scattered.

As an additional test, 56 more plots were secured and their deviations computed. Table 6 summarizes the deviations for all the plots for which these values were obtained, both the original 128 plots and the additional 56 plots. It shows how closely the curves of this large number of plots, of all ages and site qualities and selected at random, follow the polymorphic curves, and it is therefore a convincing proof of the adequacy of the polymorphic curves.

SIGNIFICANCE AND EXTENT OF THE FAILURE OF ANAMORPHIC SITE-INDEX CURVES

Unless red pine is entirely unique with respect to the fact that there is a definite and progressive change in the characteristics or form of height-over-age curves in passing from the poorest to the best sites, the anamorphic method must also produce inaccurate results with other species. As stated above, the greater the age the greater the error produced by the anamorphic curves; therefore the low ages of the plantations studied do not invalidate such a generalization.

It should be noted that the uppermost and lowermost curves for red pine (fig. 1) were purposely made (as a means of securing the proper range) to pass through the known extremes at 15 years, the age chosen for classification. It was then discovered that these curves, after passing through actual extremes at 15 years, diverged much too widely at older ages, indicating heights both higher and lower than any actually attained. If the uppermost and lowermost curves had been purposely made to pass through the known extremes at the age of say 30 years, then they would have been too close together (i. e., they would have had too narrow a range or spread) at 15 years. In this case there would be actual examples of heights at and around 15 years both greater and less than any indicated by the curves.

It can be definitely stated then that for red pine, or for species following the same general law of development, anamorphic curves can not possibly give accurate results at all ages. Such curves may be made reasonably accurate for a short distance on either side of the classification age, but the more accurate they are near that age the less accurate they are at all other ages. Specifically, if the anamorphic curves are adequate at the higher ages they will, at the lower ages, indicate too low heights for good sites and too great heights for poor sites; i. e., the curves will be too close together at the lower ages. The size of the error will increase as the age decreases. If, on the other hand, the anamorphic curves are adequate at the lower ages they will, at the higher ages, indicate too great heights for good sites and too low heights for poor sites; i. e., the curves will diverge too widely. The size of the error will increase with increase in age.

TABLE 6.—*Summary of deviations of site-index values at ages spaced five years apart, calculated from polymorphic curves*[a]

Total age[b] (years)	Values for site-index group[c] indicated								
	8.0–9.9			10.0–11.9			12.0–13.9		
	Number of deviations (total amount of deviations in parentheses)								
	Plus	0	Minus	Plus	0	Minus	Plus	0	Minus
12						1(1.0)	2(2.7)		4(10.0)
13							1(2.7)		1(5.5)
14						1(2.8)	1(0.8)		
15							2(2.8)		
16			2(1.0)	1(0.1)					
17				1(0.7)			1(0.7)		2(2.4)
21		2				1(0.1)			
26	1(0.2)		1(0.1)	1(0.2)					
31	1(0.3)		1(0.3)	1(0.1)					
Total	2(0.5)	2	4(1.4)	4(1.1)	0	3(3.9)	7(9.7)	0	7(17.9)
Average deviation	±0.24			±0.71			±1.97		

Total age[b] (years)	Values for site-index group[c] indicated								
	14.0–15.9			16.0–17.9			18.0–19.9		
	Number of deviations (total amount of deviations in parentheses)								
	Plus	0	Minus	Plus	0	Minus	Plus	0	Minus
12	7(11.0)		9(15.6)	21(47.4)	1	19(26.7)	12(22.7)		15(19.7)
13	3(6.7)		3(8.4)	11(18.6)		8(17.6)	15(17.0)		17(9.7)
14	3(5.3)		1(0.8)			2(2.9)			1(1.2)
15	3(7.7)		2(0.9)	5(8.4)		2(0.5)	9(11.2)		9(11.0)
16				1(0.2)			1(2.1)		
17	5(4.3)	2	5(3.4)	14(5.2)	3	17(10.1)	16(12.9)		19(10.0)
18	1(1.7)		1(0.4)	6(4.6)		5(3.1)	17(12.5)		15(9.3)
20							1(1.9)		
Total	22(36.7)	2	21(29.5)	58(84.4)	4	53(60.9)	71(80.3)	0	76(60.9)
Average deviation	±1.47			±1.26			±0.96		

Total age[b] (years)	Values for site-index group[c] indicated						Average deviation
	20.0–21.9			All site-index groups			
	Number of deviations (total amount of deviations in parentheses)						
	Plus	0	Minus	Plus	0	Minus	
12	3(1.8)	1	6(6.7)	45(85.6)	2	54(79.7)	±1.64
13	4(4.4)	3	3(4.0)	34(49.4)	3	32(45.2)	±1.37
14				4(6.1)		5(7.7)	±1.53
15	1(1.5)		2(0.8)	20(31.6)		15(13.2)	±1.28
16				3(2.4)		2(1.0)	±0.68
17				40(25.7)	5	47(28.7)	±0.59
18	3(1.9)		4(2.8)	29(21.6)		23(13.6)	±0.68
20	5(2.8)		2(0.8)	1(1.9)			±1.90
21					2	1(0.1)	±0.03
26				2(0.4)		1(0.1)	±0.17
31				2(0.4)		1(0.3)	±0.23
Total	16(12.4)	4	17(15.1)	180(225.1)	12	181(189.6)	
Average deviation	±0.74			±48.0	±3.5	±48.5	±1.11

[a] This is a summary of 184 plots, furnishing 373 comparisons or deviations. The 128 plots and 248 deviations of Table 1 are included.

[b] The higher of the two at which site-index values were obtained.

[c] Containing the site-index value for the higher of the two ages at which values were obtained.

As proof that red pine is by no means unique, all seven coniferous species for which height-over-age curves were constructed in the course of a yield study made in Great Britain (*4*) show development very similar to that of red pine. Incidentally, the British bulletin was not seen until the completion of the red pine study. The departure of the curves for these species from the anamorphic form is in perfect agreement with the statements of the preceding paragraph. Six species—Scotch pine, European larch, Norway spruce, Douglas fir, Corsican pine, and Sitka spruce—are classified according to height at 50 years. The set of curves for each of these six species shows the same characteristics: There is an increasingly greater spread from 50 years down to 0 year and an increasingly narrower spread from 50 years up than would be exhibited by anamorphic curves passed through the same heights at 50 years. Anamorphic curves would read too high for plots on good sites when below 50 years, too low for plots on good sites when above 50 years, too low for plots on poor sites when below 50 years, and too high for plots on poor sites when above 50 years. The remaining species, Japanese larch, is classified according to height at 15 years (as in this red pine study and for the same reason) and shows an increasingly narrower spread from 15 to 30 years, the limit of the curves, than would be shown by anamorphic curves passed through the same heights at 15 years. Here as in the red pine, anamorphic curves read too high for plots on good sites when above 15 years and too low for plots on poor sites when above 15 years.

The fundamental characteristics of the development of all these species can easily be traced on the British curves, namely, that stands on the poor sites take appreciably longer to attain their maximum rate of height growth and immediately thereafter exhibit a much less rapid decrease from that maximum rate than do stands on the good sites.

It is true that the British curves show mean height rather than average dominant height, mean height being derived from measurement of all crown classes except suppressed. This different basis, however, much as one may disagree with it, is nevertheless unlikely to affect seriously the relationship between curves of various sites. Of much greater interest is the method used in making the site-quality curves. The method is rather complicated and it will merely be noted that it is built upon the stem analysis of sample trees. Essentially, that is the method used in this red pine study.

Cajander (*3, p. 14*) states concerning mean height curves that, aside from many objections which he raises to their use in distinguishing site qualities, "they are similar to volume or yield curves in that there is not only no foundation for the practice but that there is often a distinct error involved in drawing normal curves for different quality classes with courses identical with a single mean curve [based on the entire mass of data] and with each other." This is a direct blow at the possibility of using anamorphosis in constructing mean height curves. Cajander also dismisses average dominant height as a criterion of site quality in Finland and proceeds to develop his well-known scheme of using forest types as primary site-quality classes. Within each forest type the characteristics of stem-distribution series determine the site quality. It appears later that, with a single exception, dominant height might very well be used as

a criterion of site quality but that curves of dominant height could not possibly be constructed accurately if anamorphosis were used. Cajander's statement (*3, p. 45*) is that—

> the height of dominant trees of a stand for every species of tree dealt with (except the Scots pine on the *Oxalis-Myrtillus* and *Myrtillus* types) and for every age gradation, is greater, the better a forest type is, while the current and the mean (annual) height growth reach their maximum—which is also greater—earlier, the better a forest type is.

In the light of the evidence presented and especially in view of the adoption of Bruce's (*2*) anamorphic method (in which anamorphic site-index curves are the ultimate foundation) by the Forest Service in the construction of its most recent yield tables, (those for southern pines) (*7*), the fitness of anamorphic site-index curves should be further investigated. It naturally follows that yield tables based on an incorrect classification of sites must contain errors throughout.

In the case of the recent yield tables for southern pines to which reference has just been made, there are very strong indications in Tables 64, 96, 128, and 160 of the publication that anamorphic site-index curves are no more accurate for the four southern pines than for red pine, the British conifers, or Finnish species. The tables in question show the distribution of sample plots by age and by site index for each of the four species. One would expect to find a fairly even distribution, that is, about the same proportion of very poor, poor, medium, good, and very good plots at each age. Since perfectly normal distributions are very rarely found, one would not consider it extraordinary if the distributions were more or less skewed, provided that there were no great consistency in the character of the skewness. One would certainly not expect to find with each of the four species, however, that the full range of site index was represented only by plots less than 50 years old, principally by those only 20 years old, and that all the plots over 50 years old were from medium sites only. This unexpected and peculiar distribution, nevertheless, is just what is found in the tables under discussion.

If the anamorphic site-index curves are inaccurate for the southern pines in exactly the same manner as for red pine, etc., we know that they must have too narrow a spread below 50 years (the classification age), the error in this respect increasing as the age decreases, and that they must have too wide a spread above 50 years, the error here increasing as the age increases. This being the case, there should actually be obtainable among plots less than 50 years old many heights that will be just within, at, or even beyond the upper and lower limits of the anamorphic curves and the plots will therefore be credited with very high and very low site indices, respectively, although the heights do not actually represent either such very good or such very poor sites. As with red pine and the British conifers, it is an example of the anamorphic curves reading too high for good sites and too low for poor sites below the classification age, the greatest errors being made at the lowest ages. On the other hand, there should actually be obtainable, among plots over 50 years old, no heights whatsoever to represent the highest and the lowest anamorphic site indices, the heights actually representing the best and the poorest sites occurring well within the upper and the lower limits of the anamorphic curves, and the plots therefore being credited with only medium site indices. Here we have the anamorphic curves read-

ing too low for good sites and too high for poor sites above the classification age, the greatest errors being made at the highest ages.

The assumption, therefore, that anamorphic site-index curves entirely misrepresent the actual trends, and that height growth of the four southern pines actually progresses in the same general way as does height growth of red pine in Connecticut, certain conifers in Great Britain, and Finnish species, accounts almost perfectly for the peculiar distribution shown in Tables 64, 96, 128, and 160 of the Forest Service publication on the yield of southern pines. The distribution that would be expected from such an assumption is best typified in Table 96, for longleaf pine. In this table, the oldest plots, 100 years of age or more, have a site-index range from only 70 to 80 feet (a somewhat narrower range than would probably occur if more plots were taken). For plots only 20 years old, the full range of site index, from 30 to 110 feet, is represented. From 20 to 110 years, there is an ever decreasing range of site index represented. From 50 years up only four middle site-index classes are represented; below 50 years there are plots for three poorer classes and two better classes. The other three tables show substantially the same distribution, that for shortleaf pine showing the most normal distribution. Excluding the shortleaf pine table, not one of the 64 plots having an age of 60 years or more has a site index less than 20 feet below the maximum or above the minimum site indices represented among the 20 and 30 year old plots. It seems very probable indeed that there are no old plots with indices in the uppermost and lowermost site classes, for the very good reason that no such plots ever do have high enough or low enough heights to put them in these anamorphically determined classes; the anamorphic curves diverge too widely beyond 50 years, the classification age. It will be noticed that the errors beyond 50 years are apparently much more serious than the errors below 50 years.[4]

DETERMINATION OF SITE INDEX WHEN THE EXACT TOTAL AGE IS KNOWN

When the exact total age (age of stock plus number of years planted) is definitely known, the determination of site index is very simple. It is only necessary to determine the total height of the average dominant tree and then consult either Table 3 or Figure 4. In practice in young plantations, if the most accurate possible site-index value is desired, several different total heights at several different total ages should be secured. For example, in a plantation where the trees are 20 years old it would be desirable to secure total height values not only for 20 years but also for say 17, 14, and 11 years. Four site-index values may then be found, the average of these four being a more accurate site-index value than any one value alone. To accom-

[4] In a letter to the author, Donald Bruce points out another possible explanation for the small range of site in the older southern pine yield plots; i. e., the maximum range of sites will increase as the number of plots is increased. He is inclined to attribute the peculiar distribution (which was thoroughly discussed when the Southern pine tables were being prepared) more to the scarcity of the older plots than to the defects of the anamorphic curves. He thinks it quite probable that both causes contibute to the peculiarity of the distribution. He adds: "To check this point I have just looked up similar data in McArdle's Douglas Fir Yield Table, which is soon to be published. This was based on the largest number of plots ever used for a yield table in this country, and so seemed to me particularly valuable as evidence. The site-index curves were prepared by anamorphosis and the same type of distribution within the site classes is apparent. However, the data are weak below 30 years and above 80 years. These two age classes have nearly the same number of plots, 17 and 15, respectively. I have calculated the standard deviation of the site indices for the data in these classes. It is 15.5 feet for 30 years and 19.8 for 80 years. In other words, instead of the decrease that would be expected from your hypothesis, there is an apparent increase of nearly a third. I think this is merely an accident of sampling."

plish this, in this particular case, requires measuring back at 3-year intervals. This is easy enough where the heights are obtained by climbing or by pushing up a pole or rod from below, but is of course entirely impracticable where a hypsometer is used. However, a hypsometer will probably be used mainly in rather old plantations where heights can be obtained in no other way, and in such plantations a single site-index value is sufficiently accurate. The greater the age, the less the need for refinements in the method of determining site index.

ACCURACY OF SITE-INDEX DETERMINATIONS

It may readily be calculated from the last column in Table 6 that the average difference between site-index values obtained by measuring total heights, at total ages of 7 and 12 years and of 8 and 13 years, is ±1.53 feet. The average difference between site-index values obtained by measuring at 12 and 17 years and at 13 and 18 years, is only ±0.62 foot. Clearly, site-index values in the second case are about two and one half times more reliable than those in the first case.

The average total height at any age has a standard error of ±0.3 foot. (See p. 3.) This means that about 68 per cent of these heights are within ±0.3 foot of any average value that might be obtained from an additional sample of similar data. The variations in site index that accompany variations in total height are given in Table 7.

TABLE 7.—*Approximate variation in site index corresponding to a given variation in total height*

Variation in total height (standard error in total height)	Variation in site index to nearest 0.1 foot,[a] for total ages indicated in years						
	7	10	12	15	17	20	30
Feet							
±0.1	±0.6	±0.2	±0.1	±0.1	±0.1	±0.1	±0.0
±.3	±1.8	±.7	±.4	±.3	±.3	±.2	±.1

[a] Standard error in site index.

It may be readily seen from Table 7 that site-index values derived from total heights at total ages of 12 years or more will have a standard error within ±0.5 foot (to the nearest half-foot, actually ±0.4 foot in the table), the standard error of the total heights being ±0.3 foot. In other words, about 68 per cent of site-index values derived from total heights at total ages of 12 years or more are accurate to within ±0.5 foot when the respective total height values are accurate to within ±0.3 foot.

Now, as we have just seen, the closeness with which the trend of height growth at any particular site agrees with any trend of height growth shown in the site-index curves is such that, for any plot, the site-index value for an age of 17 years or more may be expected to differ by about ±0.6 foot or less from the site-index value for the age either five years earlier or later. (See Table 6 and first paragraph of this section.) The value of ±0.6 foot was obtained entirely from 12 and 17 year and 13 and 18 year data and should be smaller for older

ages. The value may therefore be considered maximum for stands at least 17 years old.

If then we have many plots the site indices of which have been determined at say 13 and 18 years, the two site-index values for each plot may be expected to differ from each other by about ±0.6 foot, and (in about 68 per cent of the cases) either site-index value alone may be expected to be within at least ±0.5 foot (in this example about ±0.3 foot by inspection of Table 7) of any value it would have if the total height varied within the limits set by the nature of the data.

Under such conditions, the average of all site-index values for ages of 12 years or over would be statistically correct to within ±0.5 foot in a large majority of cases. However, it must be recognized that, no matter how correct statistically a given average height and the derived site index may be, there are a multitude of unmeasurable influences (climatic, biologic, etc.) that frequently deviate from the normal and thus disturb the course of normal height growth. At any particular year when height measurements are taken these influences have often had such cumulative effect as to distort to a considerable extent the average total height value that would normally have been attained at that year on that particular site.

In the study of the correlation between soil conditions and the growth of red pine, for which the site-index curves under discussion were prepared, the site index for each plot is therefore given only to the nearest full foot. In general, the site index for each plot represents the average of all site-index values for ages of 12 years and over rounded off to the nearest full foot. With plots less than 12 years old the site-index values for the greatest obtainable ages were averaged and rounded off to the nearest full foot. When the bulk of the plots are only 17 and 18 years old, as they are in this study, and even when plots are as much as 30 years old, site-index values to the nearest half foot give a wholly false conception of the accuracy attained. Only a few absolutely normal plots (normal with reference to the site-index curves) can be given a site-index value significantly accurate to the nearest half foot. For that matter, most such plots could equally well be given a site index accurate to the nearest tenth foot. Unfortunately, such plots are exceptional; the great majority of plots 30 years old or less can be site indexed with significant accuracy only to the nearest full foot.

DISTRIBUTION OF RED PINE SITE INDICES IN CONNECTICUT

It may be of interest to note the distribution of site indices encountered in this study. Table 8 shows the percentage distribution of 215 temporary plots scattered throughout the State.

TABLE 8.—*Percentage distribution of site indices in the 215 temporary plots studied*

Site index [a]	Plots	Site index [a]	Plots
	Per cent		*Per cent*
7, 8, and 9	1	18 and 19	43
10 and 11	1	20, 21 and 22	15
12 and 13	3		100
14 and 15	8		
16 and 17	29		

[a] The average site index was about 17.5 feet.

a criterion of site quality but that curves of dominant height could not possibly be constructed accurately if anamorphosis were used. Cajander's statement (*3, p. 45*) is that—

> the height of dominant trees of a stand for every species of tree dealt with (except the Scots pine on the *Oxalis-Myrtillus* and *Myrtillus* types) and for every age gradation, is greater, the better a forest type is, while the current and the mean (annual) height growth reach their maximum—which is also greater—earlier, the better a forest type is.

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When the exact total age (age of stock plus number of years planted) is definitely known, the determination of site index is very simple. It is only necessary to determine the total height of the average dominant tree and then consult either Table 3 or Figure 4. In practice in young plantations, if the most accurate possible site-index value is desired, several different total heights at several different total ages should be secured. For example, in a plantation where the trees are 20 years old it would be desirable to secure total height values not only for 20 years but also for say 17, 14, and 11 years. Four site-index values may then be found, the average of these four being a more accurate site-index value than any one value alone. To accom-

[4] In a letter to the author, Donald Bruce points out another possible explanation for the small range of site in the older southern pine yield plots; i. e., the maximum range of sites will increase as the number of plots is increased. He is inclined to attribute the peculiar distribution (which was thoroughly discussed when the Southern pine tables were being prepared) more to the scarcity of the older plots than to the defects of the anamorphic curves. He thinks it quite probable that both causes contibute to the peculiarity of the distribution. He adds: "To check this point I have just looked up similar data in McArdle's Douglas Fir Yield Table, which is soon to be published. This was based on the largest number of plots ever used for a yield table in this country, and so seemed to me particularly valuable as evidence. The site-index curves were prepared by anamorphosis and the same type of distribution within the site classes is apparent. However, the data are weak below 30 years and above 80 years. These two age classes have nearly the same number of plots, 17 and 15, respectively. I have calculated the standard deviation of the site indices for the data in these classes. It is 15.5 feet for 30 years and 19.8 for 80 years. In other words, instead of the decrease that would be expected from your hypothesis, there is an apparent increase of nearly a third. I think this is merely an accident of sampling."

plish this, in this particular case, requires measuring back at 3-year intervals. This is easy enough where the heights are obtained by climbing or by pushing up a pole or rod from below, but is of course entirely impracticable where a hypsometer is used. However, a hypsometer will probably be used mainly in rather old plantations where heights can be obtained in no other way, and in such plantations a single site-index value is sufficiently accurate. The greater the age, the less the need for refinements in the method of determining site index.

ACCURACY OF SITE-INDEX DETERMINATIONS

It may readily be calculated from the last column in Table 6 that the average difference between site-index values obtained by measuring total heights, at total ages of 7 and 12 years and of 8 and 13 years, is ±1.53 feet. The average difference between site-index values obtained by measuring at 12 and 17 years and at 13 and 18 years, is only ±0.62 foot. Clearly, site-index values in the second case are about two and one half times more reliable than those in the first case.

The average total height at any age has a standard error of ±0.3 foot. (See p. 3.) This means that about 68 per cent of these heights are within ±0.3 foot of any average value that might be obtained from an additional sample of similar data. The variations in site index that accompany variations in total height are given in Table 7.

TABLE 7.—*Approximate variation in site index corresponding to a given variation in total height*

Variation in total height (standard error in total height)	Variation in site index to nearest 0.1 foot,[a] for total ages indicated in years						
	7	10	12	15	17	20	30
Feet							
±0.1	±0.6	±0.2	±0.1	±0.1	±0.1	±0.1	±0.0
±.3	±1.8	±.7	±.4	±.3	±.3	±.2	±.1

[a] Standard error in site index.

It may be readily seen from Table 7 that site-index values derived from total heights at total ages of 12 years or more will have a standard error within ±0.5 foot (to the nearest half-foot, actually ±0.4 foot in the table), the standard error of the total heights being ±0.3 foot. In other words, about 68 per cent of site-index values derived from total heights at total ages of 12 years or more are accurate to within ±0.5 foot when the respective total height values are accurate to within ±0.3 foot.

Now, as we have just seen, the closeness with which the trend of height growth at any particular site agrees with any trend of height growth shown in the site-index curves is such that, for any plot, the site-index value for an age of 17 years or more may be expected to differ by about ±0.6 foot or less from the site-index value for the age either five years earlier or later. (See Table 6 and first paragraph of this section.) The value of ±0.6 foot was obtained entirely from 12 and 17 year and 13 and 18 year data and should be smaller for older

ages. The value may therefore be considered maximum for stands at least 17 years old.

If then we have many plots the site indices of which have been determined at say 13 and 18 years, the two site-index values for each plot may be expected to differ from each other by about ±0.6 foot, and (in about 68 per cent of the cases) either site-index value alone may be expected to be within at least ±0.5 foot (in this example about ±0.3 foot by inspection of Table 7) of any value it would have if the total height varied within the limits set by the nature of the data.

Under such conditions, the average of all site-index values for ages of 12 years or over would be statistically correct to within ±0.5 foot in a large majority of cases. However, it must be recognized that, no matter how correct statistically a given average height and the derived site index may be, there are a multitude of unmeasurable influences (climatic, biologic, etc.) that frequently deviate from the normal and thus disturb the course of normal height growth. At any particular year when height measurements are taken these influences have often had such cumulative effect as to distort to a considerable extent the average total height value that would normally have been attained at that year on that particular site.

In the study of the correlation between soil conditions and the growth of red pine, for which the site-index curves under discussion were prepared, the site index for each plot is therefore given only to the nearest full foot. In general, the site index for each plot represents the average of all site-index values for ages of 12 years and over rounded off to the nearest full foot. With plots less than 12 years old the site-index values for the greatest obtainable ages were averaged and rounded off to the nearest full foot. When the bulk of the plots are only 17 and 18 years old, as they are in this study, and even when plots are as much as 30 years old, site-index values to the nearest half foot give a wholly false conception of the accuracy attained. Only a few absolutely normal plots (normal with reference to the site-index curves) can be given a site-index value significantly accurate to the nearest half foot. For that matter, most such plots could equally well be given a site index accurate to the nearest tenth foot. Unfortunately, such plots are exceptional; the great majority of plots 30 years old or less can be site indexed with significant accuracy only to the nearest full foot.

DISTRIBUTION OF RED PINE SITE INDICES IN CONNECTICUT

It may be of interest to note the distribution of site indices encountered in this study. Table 8 shows the percentage distribution of 215 temporary plots scattered throughout the State.

TABLE 8.—*Percentage distribution of site indices in the 215 temporary plots studied*

Site index [a]	Plots	Site index [a]	Plots
	Per cent		*Per cent*
7, 8, and 9	1	18 and 19	43
10 and 11	1	20, 21 and 22	15
12 and 13	3		100
14 and 15	8		
16 and 17	29		

[a] The average site index was about 17.5 feet.

The very skewed distribution, 87 per cent of the plots falling within the upper 44 per cent of the total range of site index, is largely due to the fact that the great majority of the plots are situated on potentially agricultural soils (fine sandy loams to loams). The very poorest site indices (7, 8, 9, and 10 feet) were found only in the station's experimental plantations at Rainbow on a coarse sand. The best site indices were well distributed throughout the State.

DETERMINATION OF SITE INDEX WHEN THE EXACT TOTAL AGE IS UNKNOWN

There were many red pine plantations in the State that were of uncertain age. That is, either the year of planting or the age of the stock, or both these facts, were lacking. It was desired, nevertheless, to obtain site-index values in such of these plantations as were in good condition. Since the plantations in question were only from about 14 to 21 years old, counting the number of whorls from the top of the tree down to ground level was unsatisfactory. The total number of whorls below a 2 or 3 foot level on such trees can not be counted accurately, and the age determined in this manner may, more often than not, be one year or more out of the way. Increment borings give no better results. Between the ages of about 14 and 21 years an error of one year in age is accompanied by a corresponding error of about 2 feet (less on the poorer sites) in site index (Table 3).

Inspection of the site-index table (Table 3), however, revealed a very simple method of determining site index without knowing or even attempting to ascertain the correct age. For example, the total height of 21.4 feet is attained in 18 years with a site index of 16 feet. Given a stand in which the dominants average 21.4 feet high, we know that the site index is 16 feet if we are certain that the total age is 18 years. But if we had to count back from the tip to the ground we might determine the age as 17 years, in which case the site index would be 18 feet (17.7 exactly) instead of 16 feet, or as 19 years, in which case the site index would be only 14 feet (14.45 exactly).

The error in our count, however, would have occurred within 3 or less feet of the ground, where the whorls are more or less indeterminate. Let us, then, count the number of years that the stand needed to grow the 18.4 feet between 3 feet (from the ground level) and the top. Supposing the stand truly 18 years old and therefore of site index 16 feet, we should expect to find that there are 10.4 years of growth between 3 feet and the top (which averages 21.4 feet above the ground level). This is found by interpolating in the site-index table or from Figure 4. It will be found to be constantly true, for normal stands that follow the trend of the curves given in Figure 4, that a stand which takes 10.4 years to grow 18.4 feet above 3 feet has a site index of 16 feet. Similarly, by a series of interpolations, a stand that takes exactly 11 years to grow 18.4 feet above 3 feet has a site index of 15 feet (exactly 14.8 feet); one that takes exactly 10 years to grow that 18.4 feet has a site index of 17 feet (exactly 17 feet), and so on.

By reading complete series of such values from the site-index table, a set of curves (fig. 6) was made whereby the site index corresponding to any possible combination of the two values—total height above 3 feet and the number of years taken to grow that height, may be found. In the field, the three-feet-to-the-top method is very

easy to apply. The procedure is as follows. Select a dominant red pine and measure its total height. Count the number of years of growth between the top and a point exactly 3 feet above the ground. Do this either (1) by counting the number of internodes from the top down and estimating the remaining fraction of an internode if the 3-foot mark is not exactly at a whorl, or (2) by extracting a core with an increment borer and counting the number of years of growth. The first way is the better and quicker but becomes impractical in plantations over 20 to 25 years old. If the increment borer is used, bore at the middle of the first full internode above the 3-foot mark; the desired number of years will then be the age read on the core,

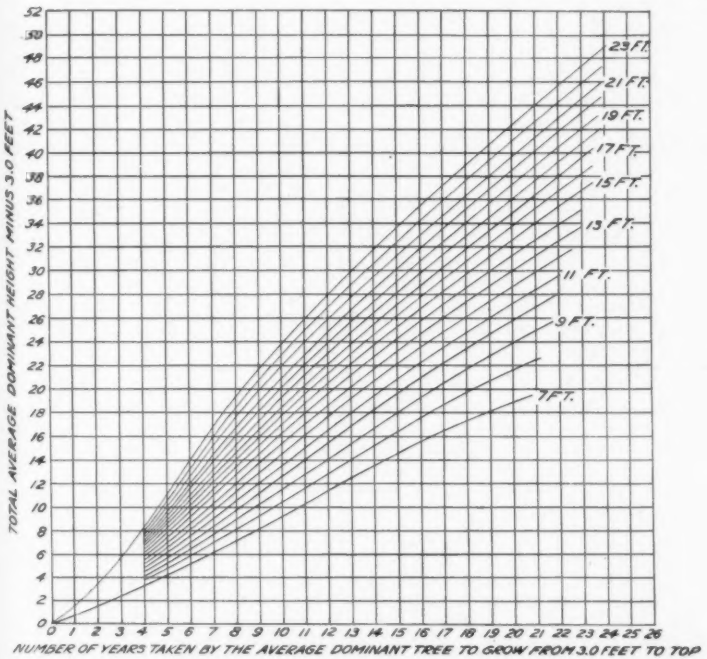

FIGURE 6.—Site-index curves for use when exact total age is unknown; (3-feet-to-the-top method). Derived from Figure 4

plus whatever fraction of an internode extends to the 3-foot mark. Repeat until enough trees have been measured to give a fair average. The more closely the two values, total height and number of years growth above 3 feet, check on different dominants the fewer trees will be needed. Ten should be a minimum number but in many cases it is all that is required. Finally, average the total heights and subtract 3 feet, average the number of years of growth above 3 feet, and refer to Figure 6.

As a test of the accuracy of this method, the site indices of 57 plots 17 and 18 years old, and of 38 plots 13, 14, and 15 years old, were determined in this way and the values compared with the "true"

site indices already obtained by the usual method of paired total-age and total-height values. The exact age of each of these test plots was known from office records and the plots were selected at random from about 170 such plots in this study.

TABLE 9.—*Comparison of the site-index values obtained by the 3-feet-to-the-top method with site-index values obtained through knowledge of the correct total age*

PLOTS 17 AND 18 YEARS OLD

Plot No. and location	Number of plots showing deviations [a] (in feet) of site index indicated					
	0	+1	−1	+2	−2	All deviations
1. Middlebury	9	3	2			14
2. Sperry Road	1	2	6			9
3. Lake Dawson	4	1	1			6
4. Wepawaug	1	1	3		1	6
5. Prospect	3	1	2			6
6. Wintergreen	3	1	1			5
7. Lake Chamberlain	2	1				3
8. Lake Watrous	1		1			2
9. Racebrook	1					1
10. Pomfret	1					1
11. Hampton				1		1
12. Bethany	1					1
13. Glen Lake	1					1
14. Wolf Den	1					1
All localities	29	10	16	1	1	57
Per cent	[b] 51	17	28	2	2	100
All localities except Nos. 2, 4, and 11	27	7	7	0	0	41
Localities 2, 4, and 11	2	3	9	1	1	16

PLOTS 13, 14 AND 15 YEARS OLD

Plot No. and location	Number of plots showing deviations [a] (in feet) of site index indicated							
	0	+1	−1	+2	−2	+3	−3	All deviations
1. Middlebury	8	4	2					14
2. Wepawaug	1	1	2		2			6
3. Mill River			1		2		2	5
4. Saltonstall			2		1			3
5. Hampton		2						3
6. Prospect	2							2
7. Wintergreen	2							2
8. Lake Dawson	1							1
9. Pomfret	1							1
10. Sperry Road			1					1
All localities	16	7	8	0	5	0	2	38
Per cent	[c] 42	19	21	0	13	0	5	100
All localities except numbers 2, 3 and 4	15	6	3	0	0	0	0	24
Localities 2, 3 and 4	1	1	5	0	5	0	2	14

[a] Deviation of site index by the 3-feet-to-the-top method from the correct site index. (A plus deviation indicates a site index better than the correct site index.)

[b] Thus: 51 per cent check exactly; 45 per cent are ±1 foot from the correct value; 4 per cent are ±2 feet from the correct value.

[c] Thus: 42 per cent check exactly; 40 per cent are ±1 foot from the correct value; 13 per cent are ±2 feet from the correct value; 5 per cent are ±3 feet from the correct value.

The results of this test are given in Table 9. It will be noted that 96 per cent of the 17 and 18 year old plots check within ±1 foot of the true site index when determined by the 3-feet-to-the-top method.

The remaining 4 per cent are within ±2 feet of the true site index. It will, however, be noted that in certain localities the 3-feet-to-the-top method produces rather constant minus errors, that is, the site index indicated is consistently poorer than the true site index. The Wepawaug and Sperry Road plots are examples of this. (Table 9.) There are two reasons for such a deviation. In the first place, a stand may get away to a much better start than is normal to the site it occupies. Unusually tall or vigorous stock, unusually good preparation or natural condition of the site, planting on land that has been recently tilled and perhaps fertilized, and unusually favorable climatic conditions for the first few years after planting are some of

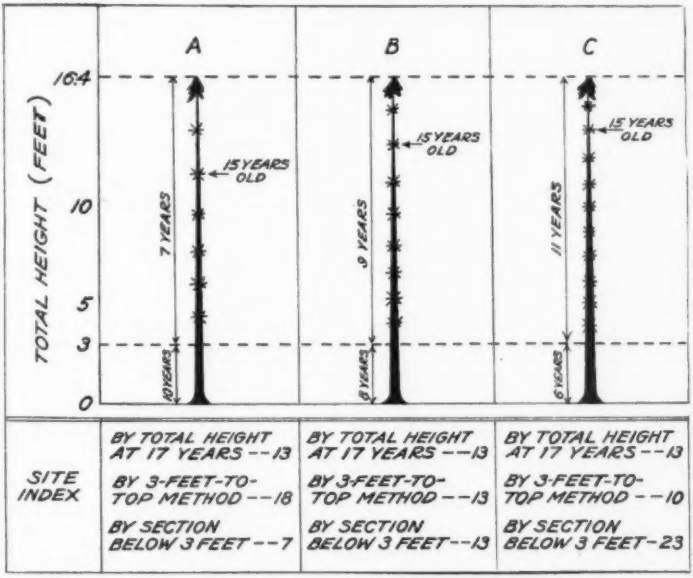

FIGURE 7.—Diagrammatic explanation of the difference that may exist between site-index values obtained by the 3-feet-to-the-top method and those obtained through knowledge of total age. Three average dominant trees are represented, each having attained a total height of 16.4 feet at 17 years total age. The examples are greatly exaggerated: A, Average dominant on a site where the growth below 3 feet is very slow and the growth above 3 feet very rapid; B, average dominant on a site where the growth both above and below 3 feet follows the average trend shown in the site-index table; C, average dominant on a site where the growth below 3 feet is very rapid and the growth above 3 feet very slow

the factors that contribute to an abnormally good start. In the second place, a stand 17 or 18 years old may have developed with such uniformity that almost every tree is a codominant, and true dominance is entirely lacking. Such a condition causes a very marked slowing up of growth; that is to say, much more marked than in the average stand as given in the site-index table. Either of these conditions has the effect of concentrating a disproportionately large number of years of growth into the section above 3 feet at the expense of the section below 3 feet. This naturally makes the site index based on the number of years of growth in the section above 3 feet seem poorer than it really is. Figure 7 shows this graphically, the situation being exaggerated to make it clearer.

The concentration of a disproportionately large number of years of growth in the section below 3 feet, and the consequent indication of a site index better than the true site index, also occur. The conditions bringing this about are the opposite of those already described—that is, abnormally poor starts and abnormally good growth 15 years or so later due to very open or irregular stands in which dominance is remarkably well expressed. Figure 7 shows this type of stand.

The 13, 14, and 15 year old plots do not check as well as the older ones: 82 per cent fall within ±1 foot of the true site index, 13 per cent are ±2 feet from the true site index, and the remaining 5 per cent are ±3 feet out. However, plots from one of the localities where consistent minus errors occurred in the test of 17 and 18 year old plantations, and plots from two additional localities previously unrepresented, account for every deviation of more than ±1 foot. The plots from the other seven localities check out very well—quite as well as the older plots. All plots from the three localities producing large deviations also checked poorly against the site-index curves shown in Figure 4.

The apparently poorer results with the younger plots are due partly to the age but mainly to the accident of location of the plots. The younger the plot the less the height and the greater the effect of abnormal conditions, which by affecting the height growth only slightly can distort the site index considerably. There appears to be no way of telling by inspection or measurement which sites or locations will produce such apparently inaccurate results when evaluated by the 3-feet-to-the-top method. However, in plantations where the 3-feet-to-the-top method gives a site-index value quite different from the value obtained from total height and total age, the former is undoubtedly the better indicator of site quality, since the abnormalities of the first few years are entirely eliminated. The 3-feet-to-the-top method is therefore preferable to the standard (total height-total age) method even when the total age is definitely known.

It thus appears that for plots up to at least 30 years old where the exact total age is unknown the 3-feet-to-the-top method of determining site index is considerably more accurate than the method of using total height and total age where the age is based wholly or partly on a count of the whorls. Even if an increment borer is used to determine age, the age of the section below the boring must be found by counting the whorls or must be estimated. Reaching the pith by boring at the ground level is always difficult and often impossible. In stands older than 30 years an error of one year in age for a given total height makes but little difference in the site index, and the older the stand the greater the allowable error in the age to obtain a given standard of accuracy in the site index. In old plantations the 3-feet-to-the-top method is not therefore entirely necessary, but its use may often result in greater accuracy. It is no harder to apply than the standard method.

The 3-feet-to-the-top method was not the only short-cut method tried. A thorough test of the determination of site index based on the number of years of growth between two fixed readily accessible height levels was made. Tables showing the number of years of growth required for dominants of each site index to progress from 3 to 9, from 3 to 13, from 4 to 10, and from 4 to 14 feet, respectively, were constructed from Table 3, and about 35 plots of known site index were

evaluated in this way. The method gave very erratic and unsatisfactory results. This is not surprising, because such a short portion of the stem and such a correspondingly small number of years of growth could hardly be expected to be truly and generally representative. With such small values a relatively slight increase or decrease results in a relatively large change in site index. Height levels materially below 3 feet are unsatisfactory because of the indeterminate character of the whorls; heights materially above 14 feet are not accessible enough to be practical.

In this connection it should be noted that when dominant trees are not more than about 14 feet high, the 3-feet-to-the-top method is unsatisfactory for the same reasons that the method just described fails. In such young or poor plantations, however, no method, not even that of total height and total age, is wholly satisfactory or by any means infallible. The development of such plantations has not proceeded far enough, or long enough, to overcome the influence on site-index determinations of abnormal conditions which can never be adequately discounted.

SUMMARY

In the course of a study of the correlation between soil conditions and the growth of red pine, it was necessary to make very accurate determinations of site quality in red-pine plantations. The plantations averaged 17 and 18 years old, in no instance exceeding 31 years old.

Anamorphic site-index curves were found to introduce large errors because they misrepresented the actual trends of growth. Accurate site-index curves for red pine can not be constructed mechanically from a single graduating curve. A polymorphic series of site-index curves was therefore constructed from seven graduating curves. This method brought out clearly the actual and marked change of trend in progressing from the poorest to the best sites. Tests of the adequacy of both series of curves are shown and the superiority of the polymorphic curves established.

Anamorphic curves indicate that the period of maximum height growth occurs between exactly the same ages for all sites; that thereafter the height growth decreases at the same proportional rate for all sites; and that the relation between the heights for any two site indices at the same age is a constant. Accurate polymorphic curves for red pine, following the individual trends of each group of sites, indicate that the period of maximum height growth occurs much earlier on the good sites than on the poor sites; that thereafter the height growth decreases at a much more rapid rate (proportionally) on the good sites than on the poor sites; and that there is no constant relation between the heights for any two site indices at the same age. Anamorphic curves for red pine based on any classification age, therefore, give too high readings for plots on good sites and too low readings for plots on poor sites below the classification age, too low readings for plots on good sites and too high readings for plots on poor sites above the classification age. This statement applies not only to red pine but also to any other species that develops in the same characteristic way. Each of seven coniferous species in Great Britain for which height-growth curves were constructed by the British Forestry Commission shows the same characteristics of development

as red pine, and consequently shows the same lack of conformity to the anamorphic principle. From the investigations of Cajander in Finland it is apparent that height curves for different sites, drawn according to the same principle as that of anamorphosis, are inaccurate and that height curves for different sites actually progress according to a general law of development exactly similar to that followed by red pine in Connecticut and by the seven conifers in Great Britain.

The observed failure of anamorphosis is important in view of the fact that the anamorphic method of constructing site-index curves is the foundation of Bruce's method for preparing yield tables, the method now adopted by the United States Forest Service. Careful analysis of the tables showing distribution of sample plots by age and by site index in a recent Forest Service publication of yield tables for southern pines, prepared by Bruce's anamorphic method, indicates the strong probability that anamorphosis produces the same errors when dealing with the four southern pines as when dealing with red pine.

Even with polymorphic curves, small plots less than 30 years old can be site indexed with significant accuracy only to the nearest full foot (at 15 years). The younger the stand the more difficult it is to obtain accurate and reliable site indices.

In Connecticut, red pine site indices range from 7 to 22 feet (at 15 years), averaging between 17 and 18 feet.

A new method is given for determining site index accurately even when the exact total age is unknown. The value and also the limitations of this method are discussed.

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A BACTERIAL DISEASE OF BARBERRY CAUSED BY PHYTOMONAS BERBERIDIS, N. SP.[1]

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INTRODUCTION

The Japanese barberry (*Berberis thunbergii*) is one of the most important ornamental shrubs grown in the northern latitudes of the United States. In general, it is not affected by diseases or by insects, and is regarded by nurserymen as a most satisfactory shrub to use for ornamental planting. However, many complaints have been received concerning certain diseased conditions of this plant. In some cases the disease starts with the blighting of a few terminal growths, followed by dwarfing and discolorations of the foliage, and finally by the death of the entire shrub. What casues this condition has never been determined. Another disease long recognized as probably due to bacteria is characterized by a severe spotting of the leaves. During the past three years the writers have made a study of this leaf spot and have definitely established it as of bacterial origin. An account of these investigations is given in this report.

PREVIOUS REFERENCES

As early as 1917 Coons [2] recognized a bacterial leaf spot of barberry, isolated the organism, and gave a brief description of the disease. His description is here quoted in full:

> For several years a bacterial leaf spot of Barberry, of Japanese, green and purple-leafed Barberry, has been noted at various places in the State. The bacterial nature [was] determined by sections, or mounts of the gummy exudations which was readily seen, usually on the under side of the diseased spot. As commonly seen the spot is about one-eighth of an inch across, usually circular and is frequently associated with a definite central lesion such as might have come from some insect attack, prick of a thorn, etc.
>
> The causal organism is a pale yellow bacillus as yet undescribed. Inoculation experiments have been made and typical spots produced from which the organism has been isolated.
>
> The disease seems more severe on the purple and green-leafed varieties, often caused marked disfiguring of these shrubs.
>
> Observations have been made for several years at M. A. C. on this disease. It has been found at North Dakota and an organism similar to the Michigan bacillus isolated. The writer has seen the same disease in barberries at Madison, Wis. It has developed on new plantings of Japanese Barberry obtained from an Ohio nursery. It is evident that we have in this leaf spot an undescribed disease which although widely distributed has so far been overlooked in the literature.
>
> Further contribution on this disease is promised.

A survey of the literature has failed to reveal any further description of the disease by this author. The organism isolated by Coons is described as yellow in culture, while the one isolated by the writers is always white.

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[1] Received for publication Dec. 8, 1930; issued July, 1931.

[2] COONS, G. H. MICHIGAN PLANT DISEASE SURVEY FOR 1917. Mich. Acad. Sci. Rpt. 20: 437. 1918.

An examination of the reports sent in to R. J. Haskell by collaborators of the Division of Mycology and Disease Survey of the United States Bureau of Plant Industry indicates that a disease supposedly of bacterial origin has been reported on a number of varieties of Berberis from many States. Whether or not these reports deal with the organism described in the following pages could not be determined, since in only a few instances were specimens available and the organism could not be isolated from these.

HOSTS AND GEOGRAPHICAL DISTRIBUTION

R. J. Haskell compiled from the reports of the plant disease survey collaborators of the United States Department of Agriculture the following list of hosts and distribution of a bacterial leaf spot of barberry. This list he forwarded to the writers on June 17, 1929.

Berberis spp.: Idaho, Michigan, Minnesota, Nebraska, New York, North Dakota, Ohio, Pennsylvania, and Washington.
B. sargentiana: New York.
B. subcaulialata: New York.
B. thunbergii: Minnesota, Missouri, New York, Ohio, and Wisconsin.
B. verruculosa: New York and Pennsylvania.
B. vulgaris: Nebraska and New York.
B. weichangensis: New York.
B. yunnanensis: New York.

He stated also that the collection files showed specimens on:

Berberis spp.: New York, Ohio, Washington, and Pennsylvania.
B. sargentiana: New York.
B. subcaulialata: New York.
B. thunbergii: Missouri and Ohio.
B. verruculosa: Pennsylvania.
B. vulgaris: New York and Washington.

In 1928 the senior author observed the disease on Japanese and common barberry in Iowa, Kansas, Minnesota, Missouri, Nebraska, North Dakota, and Wisconsin. He has since observed it on Japanese barberry in Alabama, Kentucky, Illinois, Indiana, Mississippi, North Carolina, Tennessee, Virginia, and West Virginia.

Berberis regeliana (*B. amurensis japonica*), *B. brevipaniculata*, *B. thunbergii*, and *B. vulgaris* on the University of Illinois campus were severely infected in 1929 and 1930.

SYMPTOMATOLOGY

The following description of symptoms is based on observations of the disease under natural conditions in widely separated localities at various times during the growing season, and on inoculated plants in the open. The general appearance of the disease is shown in Figure 1.

ON THE LEAVES

The spots are not located on any particular area of the leaf and they may be numerous or few. They vary from 2 to 5 mm. in diameter They are usually almost circular in outline, but on the common barberry they tend to be irregular and at times slightly angular. Shortly after the appearance of the spots the tissues turn a dark purple. Young lesions are dark green, water-soaked in appearance, and circular in outline. The under surface of the older spots has a distinct glistening appearance, probably due to exudation of the bacteria.

Both old and young leaves seem to be susceptible, for young lesions may be found at any time of the year on leaves of all ages. However, the disease shows a tendency to be most pronounced on the terminal portion of the twigs.

Defoliation does not occur in the early stages of infection, but severely infected leaves are inclined to drop off. The lack of foliage noticed on severely infected bushes, especially on the terminals, may be explained in part by the fact that the twig lesions have so weakened the stem that the buds fail to develop. (Fig. 2.) Lesions may be found also on the petioles.

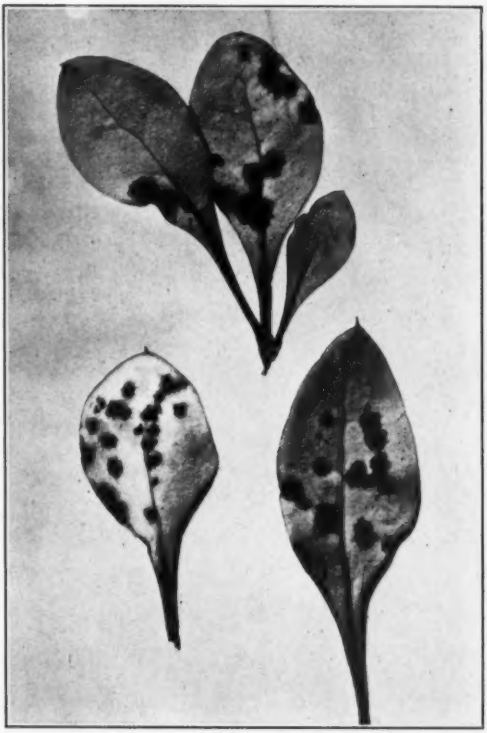

FIGURE 1.—Natural infection of Japanese barberry

ON THE TWIGS

Lesions are commonly found on the succulent twigs in the spring. When young they resemble the spots on the leaves, being circular in outline and having a water-soaked appearance. Older lesions tend to elongate and in some cases they girdle the twigs, which results in a distinct terminal blight. (Fig. 2.) The spots on the bark do not become purple as they do on the leaves.

As the twigs mature the bark tissues seem to become resistant and the spots do not enlarge. Frequently they disappear altogether, although there is evidence that the bacteria survive in the tissues.

On 1-year-old twigs in the spring another type of lesion may be found. Externally there is little, if any, evidence of the infected area, but it is usually indicated by the failure of the buds to start growth in the neighborhood of these lesions. If the grey or brown external layer of the bark is cut away near one of the undeveloped buds, small dark streaks are observed. These may be a centimeter or more in length, but usually they are much shorter, and in some cases they are mere dots. Whether these lesions originate from those on the young growth or whether they come from infection later in the season has not been determined. They are important since it is in such lesions that the bacteria appear to survive the winter.

Various other rather pronounced cankers have been observed on the twigs, some causing serious wilting by girdling the stems. It has not been possible to isolate any definite organism from these, and they are thought to be due to environmental conditions.

No infection has been found on the berries or blossoms.

ISOLATION

The causal organism was readily isolated by the dilution plate method. Sterile plates were inoculated with 1 to 5 loopfuls of a

FIGURE 2.—Infected barberry leaves below stem lesions. The infected buds failed to develop

bacterial suspension which was prepared by placing a small section of the lesion into 1 c. c. of sterile water and allowing the bacteria to ooze for a short time. The inoculated plates were then poured with melted dextrose agar which had been cooled to 40° C. After the cultures had incubated for three days at 25°, transfers from typical isolated colonies were made to dextrose-agar slants. Repeated isolations from both leaf and twig lesions yielded the same organism.

INOCULATION

On June 7, 1929, Japanese and common barberries were inoculated with a young culture of the organism. The leaves were atomized with a suspension of the pathogens while they were rubbed between the thumb and fingers. Scratching and pricking the leaves with a sharp

needle, or better still with thorns from the bush, greatly aided infection. It was observed that infection did not take place at injured areas of considerable size, but that it usually occurred at slight scratches and pricks through the epidermis. By June 20 typical leaf spots had developed on both Japanese and common barberry (fig. 3), and the organism was reisolated. A gentle rain started the day before the inoculations and continued 12 hours.

LIFE CYCLE OF THE PATHOGENE

The pathogene overwinters in lesions on young shoots. In 1930 the earliest leaf infection was found on April 15 at Urbana, Ill. The dark discolored tissue at the base of the leaves showed abundance of bacteria which were isolated in pure culture. In all original leaf infections, which were few at this time, dark discolored tissue was

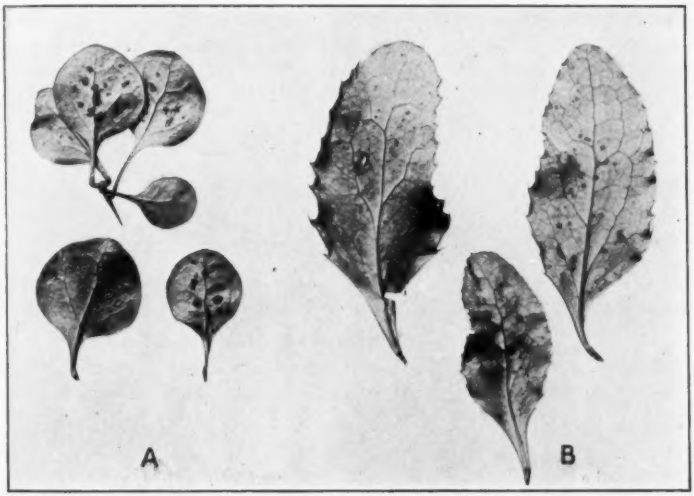

FIGURE 3.—Artificially inoculated barberry leaves after development of typical spots: A, Leaves of *Berberis thunbergii;* B, *B. vulgaris*

observed near the original bud position or on the stem less than 2 cm. from the infection. Some of the buds were killed outright but others developed severely infected leaves. (Fig. 2.)

Severe fall infection on young succulent shoots, which resembles winter injury and die-back, is characterized the following spring by the presence of bacteria in the margin of injured tissue and by the numerous leaf infections which occur near the infected portion of the shoot. (Fig. 2.)

Primary infection therefore appears to come from the bacteria which have overwintered in the twigs, and possibly the buds of the previous season. The bacteria are washed from these lesions on to the developing leaves. From the nature of this primary infection and from sections it seems certain that inoculation occurs through the stomata.

In leaf infections the bacteria after entering the stomata produce visible lesions in about one week. Microtome sections of young lesions indicated that infections originated directly beneath stomata

and spread intracellularly through the adjoining tissue. (Figs 4, A, B.) In time the bacteria gain entrance into the cells and by disintegrating the cell contents cause the tissue to collapse.

In the twigs the bacteria are largely confined to the succulent cortex. In very young tissues the bacteria often produce noticeable lesions, but as the tissues become more resistant with age the infections fail to develop rapidly. The lesions soon become inconspicuous as a result of the development of superficial tissues into which the bacteria do not advance. Since the bacteria were readily isolated from these lesions shortly after the buds opened and after primary leaf infection occurred, it is evident that this is the source of inoculum for primary infections in the spring.

Throughout the growing season secondary infections may result from the inoculum in leaf lesions. There is no evidence that the bacteria live over the winter in infected leaf débris in the soil, although such may be the case, since the organism is known to be able to withstand ice-box temperatures for five months. Infection, if at all, from this source probably occurs throughout the season but in a small degree and not until leaf infection is general.

THE PATHOGENE

MORPHOLOGY

The pathogene is a short rod 1.5μ to 2.5μ long by 0.5μ to 1.0μ wide. In the host tissue the bacteria are slightly smaller than in culture on dextrose agar. They occur singly, in pairs, and to some extent in short chains and are motile by means of two to four polar flagella. (Fig. 5.) Capsules occur in old cultures on dextrose agar, but spores were found neither in old cultures nor in lesions on leaves and shoots.

STAINING REACTIONS

The organism is Gram-positive and not acid-fast. It stains readily with carbol fuchsin and other commonly used bacteriological stains. The flagella are demonstrated clearly by Cesares-Gil's method.

CULTURAL CHARACTERS

DEXTROSE-AGAR COLONIES.—Colonies are visible on the second day, when cultures are incubated at 25° C., and by the fourth day they are 1 to 2 mm. in diameter. In time they become 5 to 6 mm. in diameter and somewhat umbonate on sparsely colonated plates. They are smooth, pulvinate, entire, white, and opaque by transmitted light.

DEXTROSE-AGAR SLANTS.—Growth is moderate, filiform at first, but later beaded, raised, smooth, white, opaque, dull in luster, butyrous in consistency, and without color in medium. Cultures from various species of Berberis were similar.

NUTRIENT BROTH.—Clouding is prompt and by the third day a slight pellicle forms. The pellicle becomes heavy in undisturbed cultures but does not connect with the tube.

PHYSIOLOGICAL CHARACTERS

LIQUEFACTION OF GELATIN.—In beef-infusion gelatin at 18° to 21° C. no liquefaction occurred. The growth was moderate, best at top, and beaded along the line of puncture. The medium was not colored.

REACTION ON LITMUS MILK.—The litmus turned slightly blue on the third day and increased to considerable alkalinity about the seventh day. No further change in color was observed. Neither coagulation and peptonization of milk nor reduction of litmus occurred.

RELATION TO FREE OXYGEN.—In agar stabs growth was best at and near the surface; there was no growth at the bottom. In agar shake cultures growth was confined to the surface.

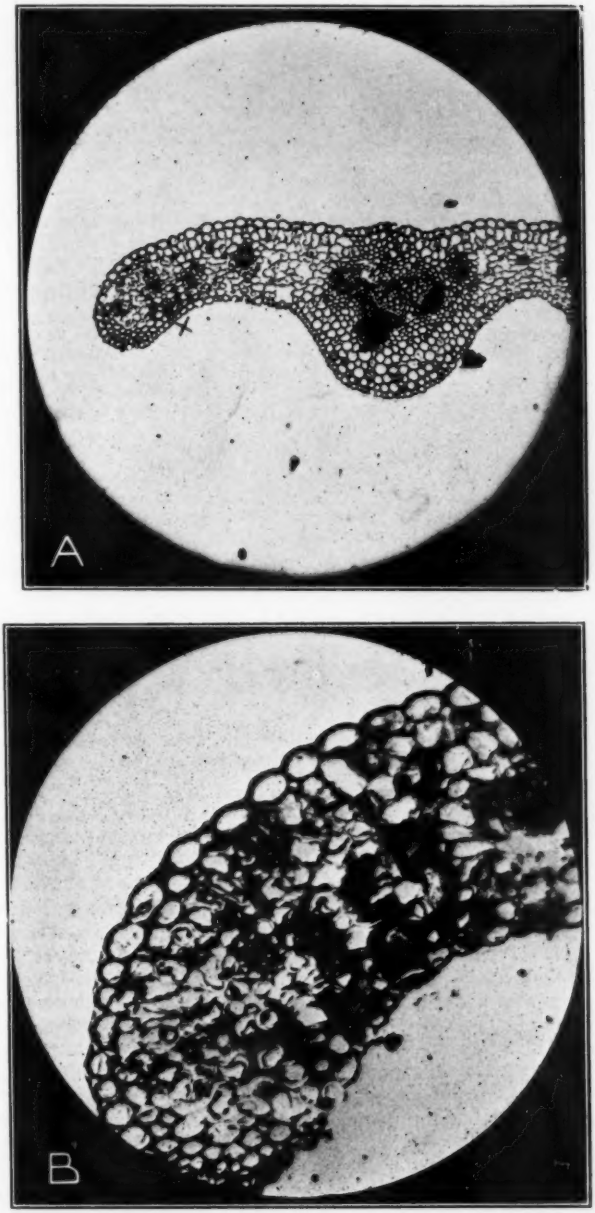

FIGURE 4.—A, Photomicrograph of a sectioned leaf lesion. The infected area (X) has spread from a substomal cavity. × 90. B, Photomicrograph of the same lesion as in A, showing extensive invasion of the mesophyll. × 740

HYDROLYSIS OF STARCH.—On starch agar plates streaked with the organism no clear zone was visible when a solution of iodine was added 10 days after inoculation.

REDUCTION OF NITRATES.—No nitrate reduction was evident in nitrate broth cultures 4, 7, and 10 days old, by the α-napthylamine sulphanilic-acid test.

PRODUCTION OF INDOL.—No indol was formed within two weeks in beef-infusion broth to which tryptophane had been added.

PRODUCTION OF HYDROGEN SULPHIDE.—In lead acetate agar no blackening of the medium occurred within two weeks.

TEMPERATURE RELATIONS.—Best growth occurred between 15° and 20° C. The minimum and maximum temperatures for growth were 7° and 30°, respectively. The thermal death point was 50° C.

FERMENTATION REACTIONS.—Growth but no gas production occurred in broth containing the following sugars, alcohols, and glucoside: Xylose, rhamnose, glucose, mannose, galactose, fructose, lactose, maltose, sucrose, rhamninose, raffinose, dextrin, inulin, glycerol, sorbitol, dulcitol, and salicin.

HYDROGEN-ION TOLERANCE.—Growth in broth was best near pH 8.5. Minimum and maximum hydrogen-ion concentrations for growth were pH 4.8 and pH 9.6, respectively.

DYE TOLERANCE.—Methyl violet, malachite green, and mercurochrome at dilutions of 1–50,000 inhibited the growth of the organism, but pararosaniline, fuchsin, eosin, and methylene blue at dilutions of 1–500 had no inhibiting effect.

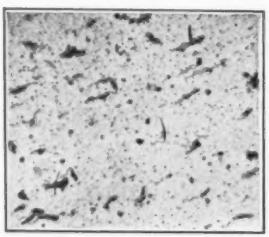

FIGURE 5.—Photomicrograph of *Phytomonas berberidis* showing polar flagella. Stained by the Cesares-Gil method. × 1,380

TECHNICAL DESCRIPTION

Phytomonas berberidis n. sp.

A short rod 1.5 μ to 2.5 μ long by 0.5 μ to 1.0 μ wide, motile by means of two to four polar flagella, occurring singly, in pairs, and in short chains but mostly in pairs. It is capsulate but forms no spores; is Gram-positive and not acid-fast; forms round entire white colonies on dextrose agar; clouds bouillon and forms a pellicle; has no diastatic action; does not liquefy gelatin; does not ferment xylose, rhamnose, glucose, mannose, galactose, fructose, lactose, maltose, sucrose, rhamninose, raffinose, dextrin, inulin, glycerol, mannitol, sorbitol, dulcitol, and salicin; produces an alkaline reaction and causes neither coagulation nor peptonization of litmus milk without reduction of litmus; produces neither hydrogen sulphide nor indol; is aerobic; optimum, minimum, and maximum pH values for growth are 8.5, 4.8, and 9.6 respectively; optimum, minimum, and maximum temperatures for growth are 18°, 7°, and 30° C., respectively, thermal death point 50°; causes a leaf spot of *B. thunbergii* and *B. vulgaris*.

A culture of *Phytomonas berberidis* has been sent to the American type culture collection, John McCormick Institute of Infectious Diseases, Chicago, Illinois.

SUMMARY

Bacterial spot of barberry has been observed on several species of Berberis in the central and mid-Western States and in Washington and Idaho. It causes darkened water-soaked spots on leaves, petioles, and young shoots.

Infection probably occurs through stomata and injuries produced by thorns.

The causal organism has been isolated from *Berberis thunbergii* and successfully inoculated into *B. thunbergii* and *B. vulgaris*.

Phytomonas berberidis is proposed as the name of the pathogene. A description of the morphological and cultural characters of the organism is given.

EUPTEROMALUS NIDULANS, A PARASITE OF THE BROWN-TAIL AND SATIN MOTHS[1]

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INTRODUCTION

Eupteromalus nidulans (Thomson) (fig. 1) is a rather small externa parasite belonging to the chalcidoid family Pteromalidae. It was introduced into Massachusetts from Europe in 1905 by the Bureau of Entomology to aid in the control of the brown-tail moth (*Nygmia phaeorrhoea* Don.). Since it has been reared both as a primary and

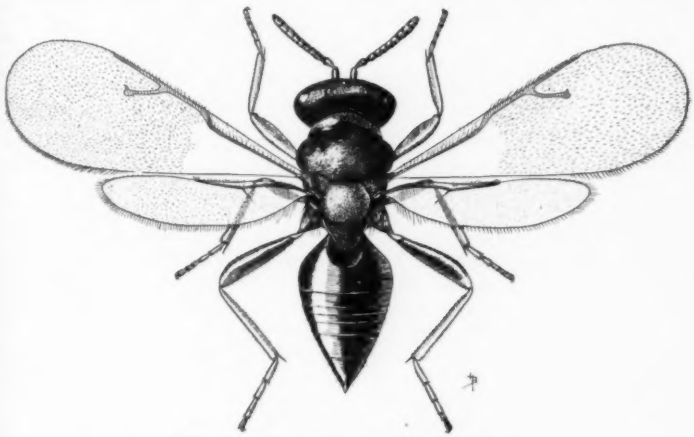

FIGURE 1.—*Eupteromalus nidulans*, female. × 23

as a secondary parasite, the following study was undertaken to provide the basis for an understanding of its greater importance as one or the other. Although general observations upon it have been made by several workers at the gipsy-moth laboratory, no detailed study of its life history has been previously attempted. For the information presented under the head of Importation and Colonization the writer has freely used notes made during a series of years by laboratory workers.

SYNONYMY

In literature the specific name *nidulans* has been quite generally attributed to Foerster, but the first published description seems to

[1] Received for publication Feb. 10, 1931; issued July, 1931.

[2] The writer is indebted to C. W. Collins, in charge of the gipsy-moth laboratory, to C. F. W. Muesebeck, under whose immediate supervision this work was carried on, to I. T. Guild and T. H. Jones for helpful criticism of the manuscript, and to H. B. Bradford for the preparation of the drawing of the adult.

be that of Thomson (*7, p. 155*)[3] in 1878, who lists the species as "*P. nidulans* (Foerster)." As a result of a misidentification in the Jardin des Plantes in Paris (*2, p. 19*), Howard and Fiske (*1*) in 1911 referred to the species as *Pteromalus egregius* Först., and this name has been used by several workers subsequently. In 1913 Kurdjumov (*2*) erected the genus Eupteromalus, designating *Pteromalus nidulans* (Förster) Thomson as genotype. Neither he nor Thomson gives any reference to a description of the species by Foerster. Kurdjumov (*2, p. 13*) says, however: "This species [*P. nidulans* Förster] was simply named by Förster, but described by C. G. Thomson." In 1927 Muesebeck and Dohanian (*4*) discuss the species briefly under the name of *Eupteromalus nidulans* (Foerst.)

The synonymy is as follows:

Eupteromalus nidulans (Thomson) Kurdjumov.
Pteromalus nidulans Thomson (*7, p. 155*).
Pteromalus egregius Howard and Fiske (*1, p. 268*). (Not *egregius* Foerster.)
Eupteromalus nidulans Kurdjumov (*2, p. 12*).
Pteromalus (*Eupteromalus*) *nidulans* Viereck (*8, p. 773*).

IMPORTATION AND COLONIZATION

As a result of a visit of L. O. Howard to Europe in 1905, the first importation of *Eupteromalus nidulans* was effected through the shipment of hibernation webs of its host, the brown-tail moth. Only a few individuals were received and none colonized. During succeeding years Eupteromalus was reared from the hibernation webs of the brown-tail moth imported from Austria, Czechoslovakia, France, Germany, Holland, Italy, Russia, and Switzerland. During the winter of 1905–6 Eupteromalus was imported in large numbers, and a total of 50,000 individuals was distributed at nine points in the vicinity of Boston, Mass. These specimens were colonized as adults early in the spring of 1906, but collections made in the following fall yielded no recoveries. Again, in the winter of 1906–7 large numbers of webs were sent to this country and from these Eupteromalus was colonized in eight additional towns, somewhat more widely separated but well within the area infested with the brown-tail moth. In the fall and early winter of 1907–8 several thousand webs of the brown-tail moth were collected from the colonization points. No specimens of Eupteromalus were reared.

In checking up the possible causes for the nonestablishment of the species, it was thought that the numbers liberated might have been insufficient and that the time of colonization might have been too early. Accordingly, in the spring of 1908 only a part of the 116,000 adults available were liberated, in six towns. On September 5 the remaining material, which had been held during the summer at a temperature of about 0° C., was colonized. Fall collections of webs from colonization points were found to contain a few specimens of Eupteromalus, but the numbers were not promising.

At this juncture it was observed early in 1909 that Eupteromalus was capable of acting as a secondary parasite, attacking the braconid *Apanteles lacteicolor* Vier., a larval parasite of the brown-tail moth. In view of the fact that this Apanteles appeared to be by far the more valuable of the two, it was decided to abandon further importations of Eupteromalus. However, 57,600 were colonized in one huge colony in the fall of 1909.

Large collections of hibernation webs of the brown-tail moth were made during the winter of 1909–10, but only a few specimens of Eupteromalus were secured from webs taken in the vicinity of the colonization points, and none at all from the points colonized in 1908. It was therefore with more or less surprise that in the following year Eupteromalus was recovered from many widely separated points. Apparently it soon spread until it became distributed over most of the area infested by the brown-tail moth. But extensive collections have indicated that until recently an average of less than 1 per cent of the larvae of the brown-tail moth have in any one year been killed in their hibernation webs by Eupteromalus.

In 1920 the satin moth (*Stilpnotia salicis* L.) was discovered near Boston, Mass., and in a comparatively short time had spread over a considerable area. In the course of a study of the control of this insect by parasites Eupteromalus was discovered in 1926 to be actively attacking it in its hibernation webs. In succeeding years the percentage of this parasitism has been increasing.

BIOLOGY AND HABITS

SEASONAL HISTORY

The following description of the seasonal activities of *Eupteromalus nidulans* is based largely upon studies of its parasitism of the satin moth. This parasite spends the winter as a full-fed larva within the hibernation web of its host. Rather early in the spring the parasite larva moves somewhat away from its host, although still remaining within the web. Here the meconium is cast and the larva pupates. In the season of 1929 pupation was first observed on April 9. By the middle of April the finding of pupae under field conditions had become general, although larvae could still be found for some time thereafter. Emergence of unparasitized larvae of *Stilpnotia salicis* from their hibernation quarters began on April 27 and continued for some two or three weeks. Adults of Eupteromalus were first observed on May 8, but were not generally abundant until the middle of May. Thus it would seem that the pupal period extended over nearly a month at this season of the year. As may be seen from the above dates, some larvae of the satin moth were still to be found in their hibernation webs for some time after adults of Eupteromalus were first found in the field. Yet general observations indicate that they are not attacked by Eupteromalus at this time.

These adults of the hibernating generation, issuing during a period of perhaps two or three weeks at about the middle of May, soon find available the cocoons of certain ichneumonoid parasites which the females of Eupteromalus may attack. Collections of the cocoons of two larval parasites of the brown-tail moth were made in order to determine whether or not they might serve as hosts for a spring generation. Cocoons of *Apanteles lacteicolor* were obtained between May 23 and May 30, and those of the first generation of *Meteorus versicolor* Wesm. were secured during the early part of June. The adult Eupteromalus reared from these collections issued between June 1 and June 15. By the beginning of July the second-generation cocoons of Meteorus were found generally present, giving these first-generation adults a fresh source of host material to attack. The

[3] Reference is made by number (italic) to Literature Cited, p. 56.

adults of Eupteromalus obtained from collections of this material issued near the end of July. Comparatively few individuals of Eupteromalus were reared from these primary parasites, however, and none were reared from later collections of any known hosts until August.

A study of the longevity of Eupteromalus indicates that 9 of the 20 females with which the experiment was begun were still alive and capable of laying eggs after four months had elapsed. Although the experiment was conducted under laboratory conditions, it seems possible that this might also occur in the field. Accordingly, adults of the hibernating generation might well be alive and able to oviposit until the early part of September. Hibernation webs of the satin moth were formed in the laboratory as early as July 24, 1929, by larvae hatching from the first egg masses collected in the field. While this is perhaps a little earlier than first web formation under natural conditions, observations showed webs to have been formed in the field in two localities in the first two weeks of August. These early webs would give any females of the hibernating generation remaining alive at this time an opportunity for oviposition before death. Adults of any generation reproducing on ichneumonoid parasites would have a longer period in which to attack the satin moth.

Eupteromalus eggs laid in these early formed webs of the satin moth produced adults in the third week of August. These adults in turn began ovipositing within a week, and the ensuing generation issued in the last week of September. Adults given access to webs in outdoor cages from September 18 to late in the fall continued to oviposit until November 15. No larvae hatching from these eggs, however, developed beyond the fifth larval instar, which is the hibernating stage. Thus it may be seen that there is a possibility of two generations of Eupteromalus upon primary parasites in the spring, and of three generations upon the satin moth in the fall, the third generation hibernating and becoming adult the following spring. There is also a possibility that there may be no reproduction upon the primary parasites, and that there may be but one or, at most, two generations upon the satin moth. In the field, however, all the generations overlap so completely that all stages of Eupteromalus may frequently be observed at one infestation at the same time. It seems probable that under field conditions Eupteromalus may more often have two rather than one or three generations in the fall upon the satin moth. It also seems possible that adults of three generations might well be ovipositing at the same time.

Eggs laid in webs held in an outdoor cage were isolated every second day and records were kept of the last date of hatching, as well as of the last date of deposition of an egg from which the larva developed to maturity. An egg laid between November 2 and November 4 was the last egg deposited to hatch, while no larvae hatching from those laid after November 1, and only a few from eggs deposited after October 25, developed to maturity.

MATING

Eupteromalus mates readily in confinement, apparently requiring no special set of conditions for the process. A newly issued male of Eupteromalus does not immediately become interested when confined with a female, but more readily seeks to mate when 24 or more

hours old. A female, on the other hand, will mate as soon as she has freed herself of the pupal skin. Since the developmental period of the male averages a day or two less than that of the female, males are usually present and active by the time the first female is ready to issue. When a male finds a female he sometimes first evinces interest by taking up a position near her and swaying his body from side to side for perhaps 5 to 10 seconds. At other times this preliminary is not engaged in, but, whether it is or not, the male approaches the female and quickly takes up a position upon her dorsum. Here he moves well forward, so that his head is directly above or a little in front of that of the female. Now the male alternately beats his wings and brings them to rest, and at the same time attempts to fold the female's antennae close to her face by tapping them with his own. When the female is ready to mate she raises her abdomen slightly and distends the ventral portion so that certain sclerites which normally are partially concealed become exposed. This movement approximately doubles the dorso-ventral diameter of the abdomen at the fourth tergite. The male now moves backward, and by grasping the female with his front legs near the posterior end of her body, he slides his abdomen, venter upward, beneath that of the female. In this position, with the head and thorax of the male at right angles to the abdomen of the female, coition takes place. This is completed in about 15 seconds, whereupon the male often returns to his original position upon the dorsum of the female. The female usually remains quiescent for a period of 20 to 25 seconds, then occupies herself for an equal length of time in cleaning her antennae and legs, and in brushing her wings. The male leaves the female as she resumes activity. When the sexes are confined together males are frequently observed to climb upon mated females and to beat their wings as if seeking to mate. However, a female has never been observed to mate a second time.

OVIPOSITION

About three days after mating the females are ready to oviposit. Occasionally the female may attempt to oviposit earlier, but no eggs are known to have been laid in such cases. Unmated females produce only males.

Oviposition has been most closely studied when the satin moth was the host, but observations have shown that the habits of the female are essentially the same when other hosts are attacked. When acting as a secondary parasite it is possible that the female does not puncture the host, since the latter is usually rather inactive. But in parasitizing the satin moth this puncturing of the host has always preceded oviposition. In an experiment in which eggs of Eupteromalus were placed upon larvae of the satin moth which had not been paralyzed by the female, the Eupteromalus larvae were unable to develop.

The satin moth spends the winter as a third-instar larva within a hibernaculum made up partly of silk and partly of the substance on which the hibernaculum is formed. The majority of these hibernacula are found on the bark of willows and poplars. Here the full-fed, second-instar larvae either cut out a hollow cell or find a crevice already present which they may or may not enlarge. This is lined with silk and a silken cover is spun for the top, into which bits of bark are often incorporated. In this hibernaculum or web the larva molts in the early fall and here it is attacked by Eupteromalus.

When the Eupteromalus female is seeking to oviposit she moves rather slowly over the surface of the bark, tapping continually with the ends of her antennae. As soon as a web is encountered she feels about on the surface with her antennae, perhaps to ascertain the position of the larva within. Then, bending her abdomen downward till the tip touches the web, she inserts her ovipositor and brings her abdomen back to a horizontal position. The ovipositor is then forced into the web by a squatting action of the female. Now she turns the ovipositor this way and that, by moving her body from side to side, the web acting as a fulcrum. If nothing is encountered, she withdraws the ovipositor and tries again in a new position. Apparently the female uses the tip of the ovipositor to learn the condition of the host within the web. If the host is dead or dried, she discovers it very soon and moves away to another web. If the host is alive, and the ovipositor touches it, the female is equally quick to perceive this. She moves the tip of the ovipositor over the surface of the larva very lightly, tapping here and there, as if to find a suitable place at which to force in the ovipositor. If she is not careful, the larva is stimulated by the prodding and moves quickly to another position in the web. When the female is satisfied as to the condition and position of the host, she suddenly thrusts the ovipositor into the larva. This produces a violent reaction, so that, in the laboratory, when the web is open in any way the larva often leaves it. Usually the female partially withdraws the ovipositor from the web, and waits about three minutes before attempting to puncture the larva again. Sometimes the egg is laid immediately after this first puncturing of the host, and one or two cases have been observed when an egg was found on a larva which was still able to react to the stimulation of the touch of a dissecting needle. But more often the female punctures the larva two or three times before an egg is laid, the host larva reacting less and less to each succeeding thrust.

This puncturing of the host by the female, preliminary to oviposition, always seems to produce a state of permanent paralysis. In the cases where an egg was found immediately after its deposition upon a larva which was still capable of movement, it has followed that the larva developed paralysis in a short time. It has been observed that hibernating larvae of the satin moth when pricked once with a micro pin show no such state of paralysis. Instead, they quickly die and become dry and much shortened. Larvae punctured by the female Eupteromalus and kept under the same conditions became dry and hard only after a considerable time had elapsed; of 48 larvae so treated that were held more than two months at room temperature, at least one was as soft as a larva newly punctured. Furthermore, these larvae punctured by the female did not shorten up as did those punctured with a micro pin. It would therefore seem that the state of paralysis produced in the larva by the female parasite is not the result of a mechanical puncture alone. No data were obtained on the cause of the paralysis, but it is suggested that possibly a substance is injected by the female. It has also been suggested that this paralysis of the host might be the result of the puncturing by the female of certain areas, such as those containing ganglia, for example. General observations indicate that the host may be punctured in nearly any part of the body, with the exception of the head, and from nearly any angle.

When the female parasite finds that the host larva will no longer react to prodding with the ovipositor, she proceeds to deposit an egg. First, she feels about over the surface of the larva with the end of her ovipositor; and then, with the ovipositor directed at the spot where the egg is to be laid, she quivers slightly. If the observer watches closely, the egg is seen to be exserted from the ovipositor at a point distant from the tip by about the length of an egg. As the egg appears, the small end issues first. Then, as more of it is exserted, it curves toward the base of the ovipositor until the entire egg lies on the outside of the ovipositor and parallel with it, the large end of the egg being toward the apex of the ovipositor. Then it is slid along the ovipositor and is usually attached to the host by the large end, which contains the cephalic end of the embryo. Under ordinary conditions all this procedure requires only about three seconds. The ovipositor does not visibly become enlarged during the passage of the egg from the body to its lower part. General observations indicate that no particular part of the host is preferred for the location of the egg.

Under laboratory conditions the female does not always oviposit upon the larva which she has punctured. Very often she leaves the web when she has succeeded in puncturing the larva, and walks about more or less. Many times she encounters another web and repeats the process of puncturing the larva, so that under laboratory conditions more paralyzed larvae without eggs are found than paralyzed larvae with eggs. Of 72 larvae which females were observed to have paralyzed, 24 were subsequently found to bear one or more eggs, and 48 had no eggs. If the female revisits a web in which the larva has become paralyzed, an egg is usually deposited without the preliminary puncturing of the host. This is believed to hold true even when another female is responsible for the paralyzing of the host larva. Because of this habit many eggs are wasted as a result of superparasitism. In the laboratory as many as 12 eggs have been deposited upon one host, while at the same time larvae in many adjacent webs were not attacked. However, the following experiment would indicate that the females prefer to oviposit upon a host which they themselves have just paralyzed. Three females were given access during a period of several days to a total of 144 webs, of which 62 contained active larvae and 82 contained previously paralyzed larvae. When the webs were examined, 56 eggs were found to have been laid in those which had contained living larvae, and 22 eggs were laid upon the paralyzed larvae.

An experiment was carried on to determine whether or not Eupteromalus would attack webs of the satin moth which contained material unsuitable for the development of the Eupteromalus larva. A total of 318 webs in each of which the host larva was dead and dried were kept with six females for a month. The webs were examined every second day, but no eggs were observed to have been laid in any web containing material of this nature. Each female regularly oviposited in adjacent webs containing live host larvae.

It has been observed that when a female is engaged in the process of oviposition she will not permit, at times at least, any interference from males or other females. If one approaches she quickly sheaths the ovipositor and darts at the intruder. Males seeking to court the female seem to be regarded with particular aversion.

FECUNDITY

To find the reproductive capacity of the female Eupteromalus, a series of experiments was carried on with 16 females. Each female was given access both to cocoons of *Apanteles melanoscelus* (Ratz.) and to webs of *Stilpnotia salicis*. Every second day these webs and cocoons were examined and the number of eggs recorded. One female laid no eggs. The largest number laid by any one individual was 583 and the average for the 16 females was 251. In general, the smallest individuals laid the fewest eggs, and the largest laid the most.

FEEDING HABITS OF THE FEMALE

Close observation of the female, while she had access to webs of the satin moth for oviposition, has shown that she feeds upon the body fluids of the host. Feeding by the female has been observed when other hosts were concerned, but no observations have been made as to how this was effected.

When the female wishes to feed she first forces the ovipositor well into the host. When the cavity is deep and the host is not near the surface of the web, she moves the host nearer by inclining the ovipositor and using it as a lever. Then the ovipositor is very slowly withdrawn from the host. As the tip of the ovipositor leaves the host, what seems to be a silvery sheen appears upon perhaps the distal third of the ovipositor itself. This sheen seems to appear a half dozen times, rhythmically. Meanwhile, the ovipositor is being gradually withdrawn from the web, and as it is lifted above the host a small white translucent tube is seen to connect it with the body of the host. When the ovipositor has been completely withdrawn from the web this feeding tube is seen to extend from the surface covering of the web to the point where the ovipositor punctured the host. This is the usual position of the feeding tube, but it was observed on one occasion that when the host was resting against the web covering, the feeding tube extended above the surface of the web. Again, when the web surface upon which the female stood while forming the tube was lifted, the tube was seen to be connected to the web at one end but failed to reach to the larva at the other. This observation would indicate that the tube originates from the parasite rather than from the host. The feeding tube is somewhat variable in length, but the tubes observed were between 0.3 and 0.5 millimeter long. Attempts at mounting these feeding tubes upon slides were unsuccessful, partly because the material of which the tube is composed seemed to become very brittle as soon as the feeding process ceased.

As soon as she completes the formation of the tube, the female turns about and applies her mouth parts to the free end of it. The tube is then seen to fill with liquid. The female feeds thus for from five to seven minutes, moving her mouth parts as she does so. On a few occasions the female has been observed to cut an opening in the web covering and to enter the web. Here she punctured the host and, waiting till it would no longer react to prodding, turned and fed at the point of insertion of the ovipositor without forming a visible feeding tube.

LONGEVITY

Studies made with a small number of females indicate that those which were fed a mixture of honey and water in the proportion of

about 1 to 5 lived longer and laid more eggs than those which had access to host material only. Females held in confinement and fed this mixture of honey and water, but allowed to oviposit only infrequently, lived longer than those kept under the same conditions but allowed to lay as many eggs as they were able. Females of the former group are known to have lived for 4 months or more, one female living for 150 days. This female laid fertile eggs at intervals until the one hundred and thirty-seventh day. Of the latter group, free to oviposit, one female lived for about 60 days, although ovipositing continually till the day of death.

Without food of any kind, the adult Eupteromalus does not live nearly so long. An experiment involving 32 adults of both sexes was conducted under laboratory conditions and at room temperature. The length of life of these individuals ranged from 5 to 19 days, both limits being represented by males. The average for the 32 individuals was about 12 days.

COMPETITION

Little is known of the results of competition between *Eupteromalus nidulans* and other secondary parasites when various primary parasites are hosts. A few preliminary observations indicate that when eggs of Eupteromalus and of *Dibrachys boucheanus* (Ratz.) of approximately the same age are placed upon the mature larva of *Apanteles melanoscelus*, Eupteromalus is the more likely to attain maturity. In the same way, competition with an undetermined species of Dibrachys for this host has in most instances resulted in the development of Eupteromalus.

When acting as a primary parasite, Eupteromalus, so far as is known, has no insect competitors. Recent observations of field conditions in a woodland infestation of the satin moth have shown that Eupteromalus may be attacked and killed by certain fungi which are attacking the hibernating larvae of the satin moth. Eupteromalus is usually killed in the larval stage.

By far the keenest competition with which Eupteromalus has to contend when acting either as a primary or as a secondary parasite is experienced with other individuals of its own kind. As has been mentioned under the discussion of the oviposition habits of the female, so many eggs are often deposited upon a single host that all the larvae issuing from them can not possibly develop to maturity. In most cases the actual cause of death of the nonmaturing individuals is probably starvation, the oldest and most rapidly developing members succeeding in obtaining most of the food material and thereby being able to complete development before the food supply is exhausted. In one or two instances a larva of Eupteromalus has been seen apparently feeding upon another larva of its own species. But the fact that two individuals may often be reared from one larva of the satin moth, even when there is not food enough for both to attain any considerable size, would suggest that cannibalism is not a general characteristic of Eupteromalus larvae.

As many as three adults of Eupteromalus have been reared from one larva of *Stilpnotia salicis*, but this condition is rare, two being the greatest number usually completing development upon one host. Seven individuals, six females and one male, constituted the largest number of adults reared from one cocoon of *Apanteles melanoscelus*.

Silvestri (*6*) noted that 29 puparia of *Voria ruralis* Fall. gave 383 individuals of "*Pteromalus nidulans* Thoms.", and that 43 cocoons of *Plusia gamma* containing larvae parasitized by Voria showed 11 to contain a female of the same hyperparasite. It seems possible, however, that this *P. nidulans* Thoms. of Silvestri may be the *P. nidulans* of Masi (*3*) which Kurdjumov (*2, p. 13*) says "does not agree well with *nidulans* Förster" (=*P. nidulans* Thomson, *7, p. 155*).

Attempts to induce the larva of Eupteromalus to migrate to hosts in other webs when competition reduced the food supply were unsuccessful. Experiments were carried on in which a paralyzed larva of the satin moth with from one to six eggs upon it was placed in a web closely surrounded by from 5 to 12 webs containing live larvae of the satin moth. Only one Eupteromalus developed in any case, and this was always on the paralyzed larva. The surrounding larvae were unaffected by any activities of the Eupteromalus larvae, so far as could be determined.

SEX RATIO

Three trees of *Populus grandidentata* Mich. were selected as samples from a fairly heavy woodland infestation of the satin moth in Kingston, N. H. These trees were cut down, divided into sections, and carefully examined in the laboratory. All the Eupteromalus larvae found hibernating in the webs of the satin moth upon these three trees were removed and held for future development. Of the number reaching maturity, 104 were males and 72 were females. A few individuals dried up when confined under laboratory conditions.

HYPERPARASITISM

Howard and Fiske (*1, p. 263, 269*) record (*Entedon*) *Pleurotropis albitarsis* (Ashm.), reared from European material, as an internal parasite of Eupteromalus. From collections made in this country *Pleurotropis nawaii* (Ashm.) has been reared in small numbers. On one occasion another member of this genus, *P. tarsalis* (Ashm.), was reared from Eupteromalus.

DESCRIPTION OF STAGES

EGG

The egg of Eupteromalus is pearly white, slightly curved, and considerably larger at one end than at the other. It bears on most of its surface many small blunt tubercles which are rather irregularly spaced. The concave surface and the ends of the egg are without tubercles. A single egg is just visible to the naked eye when upon a dark surface. Its greatest length may range from 0.33 to 0.41 millimeter, the average for 25 eggs being about 0.38 millimeter. At its greatest width it may be from 0.12 to 0.16 millimeter wide, with 0.14 millimeter as the average. The longest egg measured was the narrowest, though the shortest was not the widest. In general the larger eggs are both longer and wider than the averages. There is considerable variation in the size and shape of the eggs laid by a single female. Because of the sticky nature of the eggshell, the eggs of this species are rather easily transferred from one host to another. Considerable handling does not seem to prevent the hatching of the eggs.

In outdoor cages the egg stage may range in duration from between 1 and 2 days to as many as 14, the average length in July being about 4 days. As the egg nears the time of hatching the embryo may be seen inside. Owing to the activities of the contained larva, the eggshell is ruptured at the larger end, and the larva squirms out. Frequently the eggshell remains attached to the larva for a short time after feeding has begun.

FIRST INSTAR

The first-instar larva (fig. 2) consists of a head and 13 body segments. The head of the newly hatched larva is wider than the body, but as growth continues and the larva becomes ready to molt the body tapers toward both ends. In color the entire larva is white and opaque, although the contents of the alimentary tract are dark, and show through the body wall.

The head bears four pairs of stout, somewhat curved spines, one pair just dorsad of the labrum, one pair between and somewhat below the antennae, and the other two pairs placed ventrally and to the sides of the mouth opening. The antennae are short and rather conical, apparently consisting of one segment, and are placed well up on the head. The bases of the antennae are elevated above the surface of the head itself, giving to the larva something of a horned aspect. Upon the labrum are about five pairs of very minute structures which Parker (*5, p. 314, 317–318*) has called "sensorial organs." These structures appear under high magnification (530 diameters) as more or less circular divisions of the integument, somewhat comparable to the circular base of a spine as ordinarily observed. These organs upon the labrum have not been observed to bear spines, nor has any specific function been assigned to them. Posterior to the mouth opening and upon the ventral side of the head are about seven additional pairs of organs similar to those upon the labrum. At least two pairs have been noted as bearing each a short, slightly curved spine. Upon various other areas of the head there seem to be groups of small structures of circular outline, but these have not been given close study. The mandibles of the first instar (fig. 3, A) are long, narrow, and sharply pointed. They are rather uniformly testaceous and are strongly curved. Of 27 mandibles mounted in a similar position the minimum length was found to be about 0.016 millimeter, the maximum nearly 0.21 millimeter, and the average 0.019 millimeter. The length of a mandible in this stage was considered to be the distance from the tip to the most distant point of the base. However, the mandibles articulate with the chitinous parts of the head in such a way as to render difficult the determination of the basal limits of the mandible proper.

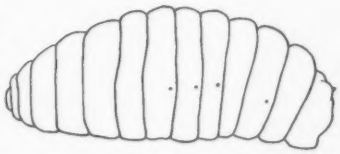

FIGURE 2.—First-instar larva of *Eupteromalus nidulans*. × 264

Each segment of the body except the last bears two pairs of small, slightly raised tubercles, from each of which arises a spine, one pair upon the dorsolateral surface and one pair upon the latero-ventral. In addition to these, each thoracic segment bears on its ventral surface a pair of spines. The thirteenth, or last, body segment appears to possess only a pair of knoblike structures laterally, which in this stage

have not been observed to have spines. The spiracles open upon the mesothoracic and first three abdominal segments, and are connected by short branches with the paired longitudinal tracheae. At the anterior margin of each of the 13 body segments are one or more rows of very small spines. These rows encircle the body, but are more or less irregular, so the number of rows is indefinite. There seems to be but one row on the anterior and posterior body segments of the larva, but perhaps three such rows on the second and third abdominal segments.

The first-instar larva, like the succeeding instars, is capable of considerable movement, which it effects by retraction and extension of the body segments. However, observations indicate that most larvae seldom leave the point of attachment to the host except during ecdysis. Even then the larva apparently resumes feeding at approximately the same spot, for the first four molt skins have frequently been removed from the area occupied by a fifth-instar larva. Frequently throughout larval life there may be observed rather rhythmic contractions of the alimentary tract. These contractions begin in the region of the junction of the mid-gut and hind-gut, and slowly move forward to the head. After a slight pause this action is repeated.

It has been observed that the first stadium may range in length from 24 to 48 hours.

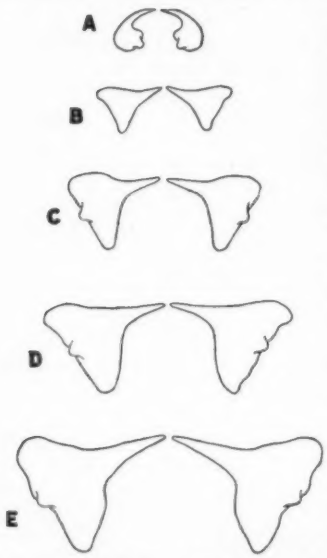

FIGURE 3.—Mandibles of *Eupteromalus nidulans*: A, First instar; B, second instar; C, third instar; D, fourth instar; E, fifth instar. All magnified 338 diameters

SECOND INSTAR

The second-instar larva does not greatly differ from the first in color, habits, or general appearance. In proportion to the body the head is somewhat smaller than in the first instar. The mandibles, however, have become larger and less sharply pointed, and have a much broader base, so their outline is quite different from that of the previous instar. They are now more or less triangular in shape. (Fig. 3, B.) Measurements of nine mandibles indicate that the minimum length of a mandible in this instar is about 0.002 millimeter, the maximum about 0.024 millimeter, and the average 0.022 millimeter. In this description the length of a mandible is considered to be the distance from the tip to the middle of the base, not including the basal tubercle, the basal limits being more plainly indicated in this and the following instars. The sensorial organs of the head have not been observed to differ in either number or position from those of the first instar. The antennae and spines, likewise, appear to be much the same.

On the body the rows of tubercles and spines are very similar, but the spiracles have increased in diameter and in number. The four

pairs of spiracles of the first instar have now been replaced by nine pairs, there being one pair each upon the mesothoracic, metathoracic, and first seven abdominal segments. This number and arrangement of the spiracles are constant for this and the following instars. The very fine spines bordering the anterior margin of the body segments have not been observed in this or in the succeeding instars.

This stadium is shorter in duration than the first, probably occupying less than 24 hours on an average.

THIRD INSTAR

The third-instar larva differs little from that of the second instar except in size. The bases of the mandibles (fig. 3, C) have become broader, and the tips more pigmented. Of 10 mandibles of this stage the minimum length was found to be 0.026 millimeter, the maximum 0.036 millimeter, and the average 0.032 millimeter. The sensorial organs and the spines of the head appear about the same in number and in position as in the previous instars, except for an additional pair of sensorial organs upon the labrum.

The duration of the third stadium is much the same as that of the second, occupying from perhaps 12 to 24 hours.

FOURTH INSTAR

The larva of this instar is very hard to distinguish from that of the third. So far as has been observed, the only appreciable difference, aside from the general increase in size, is in the greater length of the mandibles. (Fig. 3, D.) Of 14 mandibles the minimum length was about 0.035 millimeter, the maximum 0.046 millimeter, and the average 0.040 millimeter.

The duration of the fourth stadium has been observed to be about the same as that of the third, i. e., from about 12 to 24 hours.

FIFTH INSTAR

In the fifth instar the larva increases much in size, but resembles the fourth instar in many respects. The head, however, is smaller

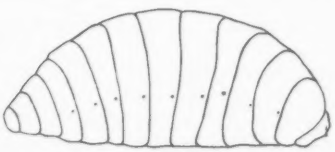

FIGURE 4.—Full-fed fifth-instar larva of *Euproctis chrysorrhoea*. Enlarged about 28 diameters.

FIGURE 5.—Antenna of fifth-instar larva of *Euproctis chrysorrhoea*. × 1500

in proportion to the rest of the body, so the full-fed larva (fig. 4) tapers almost equally toward either end, the fore part being a bit more blunt than the hind part. The larva may vary considerably in size, depending upon conditions obtaining during its development, one of the most important of which is the character and the quantity of food material available. Measurements of 102 larvae placed the limits of variation in the length of the body at 0.96 millimeter as a minimum and 2.6 millimeters as a maximum, the average length being 1.5 millimeters. The antennae (fig. 5) still appear to be 1-segmented,

although they are somewhat longer in proportion to their width than in the earlier instars. They are light yellowish to light brown in color. The spines of the head seem to coincide in number and in position with those of the previous instars. The labrum in the mature larva appears to have six pairs of sensorial organs, as in the preceding two instars. But the number of pairs of these organs upon the ventral side of the head seems now to be eight, of which at least four pairs bear spines. The mandibles (fig. 3, E) are considerably larger than in the fourth instar, measurements of 24 indicating that the minimum length is about 0.045 millimeter, the maximum length 0.057 millimeter, and the average 0.050 millimeter.

The rows of tubercles upon the body segments are much as described for the first-instar larva, except that now they are smaller in proportion to the size of the larva.

When the larva is full-fed it moves away from the host somewhat, within the confines of the web or cocoon, and remains inactive. It is at this time that the mid-gut opens posteriorly, so that the waste material which has accumulated during larval life may be voided. This material, the so-called meconium, is black and rather characteristically molded so that it resembles a string of closely strung beads. Soon after the meconium is voided the larva takes on pupal characters and the larval skin is cast off.

Except in the case of the hibernating generation, the fifth stadium, including the period of rest sometimes called the prepupal period, may be as short as 7 days and often as long as 8 to 10 days. The period of growth of this stadium is about two days, or similar to that of the first stadium. In the hibernating generation the time spent in the fifth stadium may be as much as seven or eight months.

PUPA

When first formed the pupa is almost white, later darkening through yellow and brown to black. Being somewhat sticky, it adheres to the host or to the walls surrounding it. It is naked and incapable of movement. To the posterior end of the body there is usually attached the exuvium of the fifth-instar larva.

The pupa seems to be rather tolerant of the winter temperatures at Melrose Highlands, Mass., for of 20 pupae removed from the laboratory at room temperature to an outdoor cage on December 27, 1928, eight completed their development the following spring. The pupal period normally ranges in length from 9 to 12 days under favorable conditions, but in the case just mentioned the adults issued after four months in the pupal stage. In the field, however, hibernation in the pupal stage has never been observed.

HOST RELATIONS

EXPERIMENTAL EVIDENCE AS TO SELECTION OF HOST

Since Eupteromalus is known to be both a primary parasite upon *Stilpnotia salicis* and a secondary parasite upon *Apanteles melanoscelus*, an experiment was undertaken to determine in which rôle it played the more important part. The number of eggs deposited upon one or the other host when both were equally available was taken to be a fair criterion of the parasite's response. Since an equal number

of cocoons and webs were not available,[4] a known number of hibernation webs of *S. salicis* and of second-generation cocoons of *A. melanoscelus* were submitted together to each of 15 female Eupteromalus. The results are shown in Table 1.

TABLE 1.—*Comparison of oviposition by Eupteromalus nidulans upon Stilpnotia salicis and Apanteles melanoscelus*

Female No. [a]	Period of oviposition	Webs of S. salicis exposed	Eggs laid in webs	Cocoons of A. melanoscelus exposed	Eggs laid in cocoons	Total eggs laid
	Days	*Number*	*Number*	*Number*	*Number*	*Number*
1	8	56	38	12	3	41
2	15	83	43	18	0	43
3	32	187	219	37	0	219
4	29	181	218	34	54	272
5	44	198	148	49	76	224
6	26	130	127	29	0	127
7	21	94	101	25	14	115
8	25	142	140	28	31	171
9	67	178	2	77	234	236
10	33	155	154	34	32	186
11	24	121	97	25	0	97
12	28	145	118	32	1	119
13	26	139	108	29	0	108
14	44	185	140	51	216	356
15	19	81	53	21	0	53
Total	441	2,075	1,706	501	661	2,367

[a] Females numbered 1, 2, 3, 4, and 14 were reared upon *A. melanoscelus*, the others upon *S. salicis*. Females numbered 1, 2, 3, 4, 5, and 7 had oviposited in webs of *S. salicis* before the beginning of this experiment.

It is found that in the case of 13 of the 15 females more eggs were laid in webs than in cocoons, while in the case of 2 females more eggs were laid in cocoons. In all, 1,706 eggs were laid in webs and 661 in cocoons. But in this experiment equal numbers of webs and cocoons were not available, consequently 2,075 webs and 501 cocoons were supplied to the 15 females. Now, if egg deposition upon one or the other host were dependent upon chance alone, there should be 4.1 times as many eggs laid in webs as in cocoons $\left(\frac{2,075}{501}=4.1\right)$, while as a matter of fact there proved to be but 2.6 times as many $\left(\frac{1,706}{661}=2.6\right)$. Viewed in the light of this result, the experiment indicates that these females showed a slight preference for the cocoons of *Apanteles melanoscelus*. But of the 661 eggs laid in cocoons by the 15 females, 450 (or about 68 per cent) were laid by the 2 females numbered 9 and 14. The results obtained from these two females, differing so much from those of the other 13, indicate that further experiments, even if conducted in exactly the same manner, might yield a very different ratio between the average number of eggs laid in webs as compared with eggs laid in cocoons. It seems plain, therefore, that a satisfactory test of "preference" would require the employment of a much larger number of females.

[4] As another phase of this experiment (summarized above under the discussion of fecundity), it was desired to learn the greatest number of eggs which each female was capable of depositing. In this connection it was thought well to provide each female with more host material than it was possible for her to utilize. Because of the limited number of cocoons of *A. melanoscelus*, this excess of host material was represented by webs of *S. salicis*, hence the larger number of webs over cocoons used in this experiment.

Conditions were not similar for the various females in the following three respects: (1) Not all of the 15 females were reared from the same host, for Nos. 1, 2, 3, 4, and 14 were bred from *Apanteles melanoscelus* while the other 10 were bred from *Stilpnotia salicis*. (2) In regard to mating, all of the females were observed in coition except No. 15, which reproduced parthenogenetically. (3) Females Nos. 1, 2, 3, 4, 5, and 7 had oviposited in webs of *S. salicis* previous to this experiment, while the other 9 females had not. Also, it should be observed that no cocoons of *A. melanoscelus* were provided for the former group of 6 females before the beginning of this experiment, so that a habit of ovipositing in webs might have been formed.

Attention is called to the close similarity between the records for females 3 and 4, and between those for females 5 and 14. It will be seen that the length of the oviposition period, the number of webs submitted, the number of eggs laid in webs, and the number of cocoons given the female are much the same for each member of the respective pairs. No. 3 differs from No. 4, and No. 5 from No. 14, however, in the number of eggs laid in cocoons, and, of course, in the resulting total of eggs laid. It would seem from these examples that the variability of the females in regard to ovipositing upon one or the other host is so great, even between females similar in other respects, that the results of this experiment can not be regarded as in any way conclusive.

Laboratory conditions under which experiments are carried on, no matter how well conceived these experiments may be, are seldom true reproductions of field conditions. In general, then, field experiments offer more reliable sources of data. The rest of this paper deals with information obtained from field observations, at least some of which were on a sufficiently large scale to be conclusive.

THE IMPORTANCE OF EUPTEROMALUS AS A SECONDARY PARASITE

In connection with various phases of experimental work at the gipsy-moth laboratory, the collections mentioned in the following paragraphs were made by members of the laboratory personnel at various points within the areas in New England infested with the gipsy and brown-tail moths.

Collections of the first-generation cocoons of *Apanteles melanoscelus*, a common parasite of the gipsy moth, have been made during a period of several years. Of a total number of 1,488, from at least nine localities, none has given Eupteromalus as a secondary parasite. These were collected as near the time of issuance of the Apanteles adults as was practicable, so that the cocoons might be subject to the greatest amount of secondary parasitism.

Large collections of the second-generation cocoons of *Apanteles melanoscelus* have also been made, and during a longer series of years. A total of 98,700 has been isolated and held for observation, representing collections from 30 localities. Only a single cocoon is recorded as having given Eupteromalus. Records indicate, however, that a large part of this total number collected represents material which was brought in from the field very soon after the cocoons were formed, leaving little opportunity for the secondary parasites to attack.

From collections of hibernation webs of the brown-tail moth, a total of 443 cocoons of *Apanteles lacteicolor* was removed. These had been

subject to secondary parasitism until nearly time for the Apanteles adults to issue. After being held until the secondary parasites had ceased issuing, these isolated cocoons showed Eupteromalus to have issued from six, or from a little more than 1 per cent of the total.

A total of 304 cocoons of the first and second generations of *Meteorus versicolor* gave two Eupteromalus, or about two-thirds of 1 per cent secondary parasitism.

Still another known host was collected at infestations of the brown-tail moth in the form of 80 puparia of the tachinid *Compsilura concinnata* Meig. These puparia, although heavily parasitized by other secondaries, yielded no Eupteromalus.

Six collections of another tachinid parasite of the brown-tail moth, *Sturmia nidicola* Town., yielded 473 puparia, none giving Eupteromalus.

Among these species are included the hosts upon which Eupteromalus has been recorded as a secondary parasite. From the information obtained from these collections, however, it seems that Eupteromalus is not an important secondary parasite of any of these hosts.

IMPORTANCE OF EUPTEROMALUS AS A PRIMARY PARASITE

Although Eupteromalus larvae have been found in the hibernation webs of the brown-tail moth from localities rather well distributed over the infested areas each year during a period of some 20 years, the extent of such parasitism seems to be of small importance. Some webs will show very many more of the parasites present than will others, the number ranging from none to several hundred per web. But the number of host larvae in these webs is large, ranging from 5 to 2,800 or 2,900, the average being well over 300. The records show that the percentage of parasitism of this host by Eupteromalus is seldom more than 1 per cent over the whole area. Since 1926, when Eupteromalus was found attacking the satin moth, the percentage of its parasitism of the brown-tail moth has been increasing.

Upon the satin moth the percentage of parasitism seems to be increasing over the New England area as a whole. Early in the spring of 1927, before development of either parasite or host had begun, examination of 6,429 hibernation webs of the host showed 154 to contain Eupteromalus, a result indicating about 2.4 per cent parasitism by the hibernating generation. Included in this total number of webs examined were many containing dead host larvae, which observations have indicated may have died soon after the formation of the web. Since experiments have shown that Eupteromalus does not attack these webs, it would seem that the real effectiveness of Eupteromalus was much greater than the percentage 2.4 would indicate. Again, this figure relates only to the hibernating generation of Eupteromalus, and observations show that many of the host larvae are killed by a generation previous to the hibernating generation. Besides, we do not know the amount of control exercised upon the host by the female in her habits of puncturing the larva and then leaving the web without ovipositing, or by feeding upon the host larva. These conditions obtain also in the three cases about to be considered, unless otherwise indicated.

In 1928 examinations of the hibernation webs were made in 10 townships scattered over the infested area. The method was to open

the first 100 webs encountered and to record the contents, only live host larvae and parasite larvae being included in this count. There were 1,067 webs examined in this way, of which 126 were found to contain Eupteromalus of the hibernating generation. This attempt to approximate more nearly the true percentage of parasitism by Eupteromalus gives a figure of 11.8 for the entire infested area. The examinations in some localities showed Eupteromalus to be absent, while those in others indicated a percentage of parasitism as high as 58.

In 1929 webs were examined in 21 townships, some of which were upon the border of the infested area. A total of 1,674 were examined in the same way as in the preceding year, and 153 (or about 9 per cent) of these were found to contain hibernating Eupteromalus. The parasitism in individual localities ranged from none at all to as much as 52 per cent. Of the 21 townships, Eupteromalus was found in 12.

In connection with another experiment, a rather thorough examination of all the hibernation webs to be found upon an entire tree was made at a woodland infestation of the satin moth. The infestation was upon a group of about 500 trees of *Populus grandidentata* which were from 40 to 60 feet in height. Three trees were chosen as samples, cut down, and brought into the laboratory in sections. Here they were carefully examined by members of the laboratory staff and the contents of all webs found were noted. From the results so obtained, it was found that there was upon each tree an average of 1,695 webs of the present year. Death of the host larva could be definitely attributed to Eupteromalus in an average of 666 webs per tree. This average gives about 39 per cent parasitism by Eupteromalus under these conditions.

CONCLUSIONS

From the foregoing figures one would conclude that Eupteromalus is of slight importance as a parasite of the brown-tail moth. As a parasite of the satin moth, however, it seems to show some promise. Although the percentage of parasitism over the entire area has not had a constant or marked increase during the years in which this parasitism has been studied, there undoubtedly was an increase between 1926 and 1929. It seems reasonable to expect that the parasite will follow the host as the latter spreads to its climatic limits, and that as the parasite catches up with the host the average percentage of parasitism will increase. Consequently, if the present rate of increase continues, the percentage of parasitism of the hibernating stage of *Stilpnotia salicis* by Eupteromalus will become of greater economic importance.

SUMMARY

Eupteromalus nidulans (Thomson) was first introduced into this country in 1905 to assist in controlling the brown-tail moth (*Nygmia phaeorrhoea* Don.). As a result of a misidentification (*2*), this parasite has been referred to by various workers as *Pteromalus egregius* Föerst. Although rather large numbers of imported material were colonized during the years 1906 to 1909, establishment of the species was not proved until more than four years after the first colonization. Records of wide dispersion were obtained very soon thereafter. In 1909 it was discovered acting as a secondary parasite upon *Apanteles*

lacteicolor Vier., and further colonization was stopped. In 1926 Eupteromalus was found attacking the satin moth (*Stilpnotia salicis* L.), which had been known to occur in Massachusetts since 1920.

Eupteromalus hibernates as a mature larva within the web or cocoon of its host. There may be as many as two generations each year upon primary parasites in the spring, and as many as three generations, the third hibernating in the fifth larval instar, upon the satin moth in the fall. Again, there may be no reproduction upon primary parasites, and but one or two generations on the satin moth in the fall. The adults mate readily in confinement. The females oviposit only upon host material which is suitable for food for the larvae. The female will oviposit readily whether mated or not, parthenogenetic reproduction producing only males. The oviposition habits of the female show that the host seems always to be punctured before eggs are laid, and that this puncturing produces a paralysis in the host which does not seem to be the result of a mechanical injury alone. The eggs are deposited upon the surface of the host, no definite part of the body being preferred for the location of the egg. Superparasitism is common, while hosts are frequently paralyzed but no eggs are laid. The paralysis of the hibernating larvae of the satin moth is permanent. The average number of eggs laid by 16 females was 251.

The females form a feeding tube through which the body fluid of the host is obtained. Unfed adults lived an average of 12 days, while some of those fed upon a mixture of honey and water lived as long as 150 days, the average being considerably less.

Little is known regarding competition with other parasites, but Eupteromalus was the successful species in the cases observed. One Eupteromalus is usually reared from a single larva of *Stilpnotia salicis*, although as many as three have been noted. Seven is the largest number of individuals observed to develop to maturity on one larva of *Apanteles melanoscelus* (Ratz.). The larva of *Eupteromalus nidulans* does not migrate from one web of the satin moth to another. A field observation showed 104 males and 72 females to be the sex ratio present.

The eggs of *Eupteromalus nidulans* average 0.38 millimeter in length, and adhere readily to nearly any surface. There are five larval instars, the first possessing four pairs of spiracles and sickle-shaped mandibles which combine to separate it from the following instars. These latter instars are alike in having nine pairs of spiracles, and mandibles much less strongly curved. The naked pupa adheres to the host or to the surrounding walls of the web or cocoon.

In a laboratory experiment to determine whether Eupteromalus laid more eggs in webs of *Stilpnotia salicis* or in cocoons of *Apanteles melanoscelus*, the variation between the results obtained from individual females was so great and the number of females in the experiment was so small that the results are inconclusive. From field collections of primary parasites recorded as, or likely to be, hosts of Eupteromalus, it was found that Eupteromalus was not an important secondary parasite of any of them. Upon the brown-tail moth, Eupteromalus has rarely exceeded a parasitism of 1 per cent over the infested area as a whole. As a parasite of the satin moth, it shows considerable promise. During the years 1926 to 1929 the average

percentage of parasitism over the entire infested area increased from about 2.4 to about 9. In a field experiment in the case of a woodland infestation Eupteromalus was found to have killed 39 per cent of the hibernating larvae of the satin moth.

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A SEED CATERPILLAR, GRAPHOLITHA CONVERSANA WLSM., ON A NATIVE CLOVER IN THE NORTH PACIFIC REGION[1]

By L. P. ROCKWOOD, *Entomologist*, and SARAH K. ZIMMERMAN,[2] *Assistant Entomologist, Division of Cereal and Forage Insects, Bureau of Entomology, United States Department of Agriculture*

INTRODUCTION

In the history of economic entomology it has several times been recorded that insects have deserted their native host plants to feed principally upon nearly related cultivated crops, upon which they have become pests of major importance, even in regions far from their original habitats. The manner of most such adaptations is lost in the obscurity of prehistoric time and can only be inferred.

The native flora of the North Pacific region is rich in species of Leguminosae, whereas the development of an agricultural practice that includes legume culture is recent in that region. Reflection on these facts has led the writers to make incidental observations on insects associated with native legumes, with the idea that some of them may develop into pests of cultivated forage crops.

On July 12, 1920, near Nehalem, Oreg., the senior writer observed small lepidopterous larvae on the flower heads of a native clover which grew in some abundance in low, moist places between the sand dunes a few hundred yards from the ocean beach. These caterpillars had very greatly reduced the production of seed. Specimens were collected and reared, and when the adult moth emerged the following April it was found[3] to be *Grapholitha conversana* Wlsm. (*Laspeyresia wana* Kearfott).[4] Since that date the junior writer has studied the species and accumulated considerable information on its seasonal history and the stages in its life history.

As the insect has already been found occasionally on red clover, there is a possibility that it may become adapted to the cultivated clovers, alsike, red, or white. In that eventuality the Pacific Northwest would have what it has hitherto been spared, a clover pest comparable to the clover seed caterpillar of the Eastern States (*Enarmonia*) *Grapholitha interstinctana* Clemens (*1, 9*).[5]

HISTORY AND DISTRIBUTION OF THE SPECIES

The synonymy of *Grapholitha conversana* Walsingham is given by Heinrich (*2, p. 33*).

G. conversana was described in 1879 by Lord Walsingham from "Camp Watson, on John Day's River, Oreg." (*2, p. 34*). According to a military map of the Department of the Columbia (*7*), this locality is about 10 miles east of Mitchell, where the old Dalles military road

[1] Received for publication Jan. 15, 1931; issued July, 1931.
[2] Resigned Mar. 7, 1929; appointed collaborator Mar. 16, 1929.
[3] Determined by Carl Heinrich.
[4] Order Lepidoptera, family Olethreutidae, subfamily Laspeyresiinae.
[5] Reference is made by number (italic) to Literature Cited, p. 65.

crossed Badger Creek in what is now Wheeler County. Kearfott (*4, p. 60*) in 1907 described the species as *Enarmonia wana* from Carmel, Calif., and gave as an additional locality San Luis Obispo, Calif.

Heinrich (*2, p. 34*) gives the distribution of the species as California, Oregon, Washington, and British Columbia. The present writers have collected the species from its native host near the seacoast in Tillamook and Clatsop Counties, Oreg. H. K. Plank collected specimens [6] at Seaview, Wash. The writers have not yet had an opportunity to search for this insect and its native host in the region east of the Cascade Mountains.

DESCRIPTION

THE MOTH

Kearfott (*4, p. 60–61*) describes the moth as follows:

Enarmonia wana sp. nov.

Expanse 10–12 mm.

Head: Gray, speckled with darker gray; palpi pale cinereous, upper end of tuft a shade darker, outer joint blackish; antenna gray with darker annulations at joints, thorax bronzy-brown, with a reddish-green tinge; abdomen shining blackish-fuscous above, paler beneath, anal tuft whitish; legs whitish-gray, shining iridescent scales.

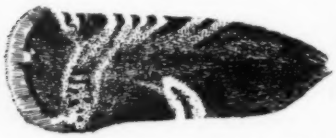

FIGURE 1.—*Grapholitha conversana:* Fore wing of adult. × 10

Forewing (fig. 1): Shining bronzy-brown. Before the middle are three white costal dashes, the inner one nearly obsolete, each continuing to top of cell in lines of leaden-metallic. Beyond the middle are three pairs of white costal dashes, the two inner pairs close together, the outer close to the apex, all are continuous as golden-metallic lines to a third below costa. The ocellic spot is olivaceous-yellow, crossed by four horizontal black lines; the vertical side-bars are golden-metallic, the inner one connecting with first costal line beyond middle. The dorsal white patch, which is divided by a brown dot on dorsum, about three times as long as wide, curving outward slightly and reaching but a trifle above fold; from the outer upper edge it is continued as a metallic line to above middle of wing approaching but not joining the metallic line from costal spot before middle. The tips of the scales on upper half to middle, in apex and before termen are tipped with yellow. There is a dark brown terminal line cut by a white dash below apex. Cilia shining fuscous.

Hindwing: Bronzy-brown, paler toward base, cilia same inwardly, white outwardly; underside shining gray-white.

Underside forewing: Shining bronzy-brown, with costal spots repeated. In certain lights there is a greenish bloom over both surfaces of both wings.

About fifty specimens: Carmel-by-the-Sea, Monterey Co., Cal., April; San Luis Obispo, Cal., March; all collected by A. H. Vachell.

Heinrich (*2, figs. 125, 299*) has figured the male and female genitalia, and remarked (*2, p. 33–34*) that—

> The cornuti in *conversana* are arranged upon a horseshoe-shaped chitinous band and are all deciduous except one rather slender spine which is fixed at one of the tips of the band. The wing pattern is somewhat variable. In a large reared series from Oregon in the National Museum some specimens show but faint traces of the dorsal white marks and a few are entirely without them. Normally, however, the dorsal white geminations are present and sharply defined. The abnormal specimens will run to *caeruleana* in our key, but can be separated by their genitalia. * * * Hind wing with veins 3 and 4 connate or very short stalked. * * * Alar expanse 8–12 mm.

[6] Pinned specimens on file in the Division of Deciduous Fruit Insects, U. S. Bureau of Entomology, are labeled "June, 1918, from cranberry."

He also stated (*2, p. 33*) that this Pacific coast species resembles (except for the genitalia) the eastern *fana* which has been reared from the flower heads and terminal buds of the leguminous plant Meibomia.

THE EGG

The egg (fig. 2) is scalelike, oval, slightly convex on the upper side, flat on attached side, finely granulate, with low wrinklelike ridges extending from sides toward center. The outside coating of the egg, which overlaps on the plant as a hyaline lacy margin, is gluelike, coarsely reticulated, and iridescent. The egg measures 0.59 by 0.39 mm. (Specimen from alcohol attached to clover bract.)

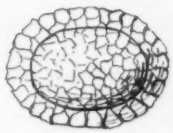

FIGURE 2.—*Grapholitha conversana:* Egg. × 40

THE LARVA

The larva is cylindrical, without secondary hair, the color ranging from white to pinkish. The legs and prolegs are normal. The crochets (16–26) are uniordinal, in a complete circle except those on anal proleg, which are in an arc of about 200°. The setal areas (fig. 3) are pallid and lightly chitinized, as are the thoracic legs, which in the early stages are mostly fuscous. The thoracic shield is broad, shining, warm buff mottled with tawny, the mid-dorsal line narrow, pallid. This shield is fuscous black in the early stages and the anal shield also is darkened. The spiracles are narrowly black rimmed, small, circular, slightly produced; the spiracle on the prothorax is about one-third larger than those of abdominal segments 1–8, which are subequal. The body, except the chitinized areas, is densely covered with fine aculei (as seen under high magnification).

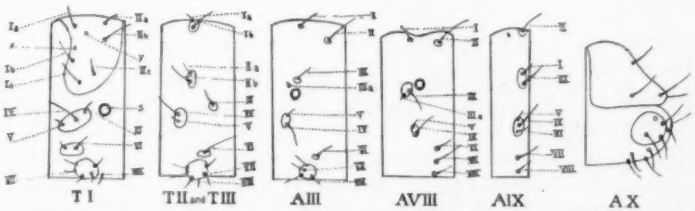

FIGURE 3.—*Grapholitha conversana:* Setal map of mature larva, AIII, AVIII, AIX, AX, third, eighth, ninth, and tenth abdominal segments, respectively; TI, prothorax: TII and TIII, mesothorax and metathorax; s, spiracle; x and y, punctures

The body setae are pale, fine, obscure. On the prothorax the setae Ia and Ib are near and Ic is behind the anterior margin of the shield; IIa is caudad and barely mesad of Ia; IIb is directly ventrad of and close to IIa; IIc is nearer to Ic than to Ib; the prespiracular chitinization is oval, ventro-cephalad of the spiracle, bearing three setae (III, IV, and V); group VI is bisetose on the prothorax, unisetose on the mesothorax and metathorax. Abdominal segments 1 to 7 have II longer than and ventro-caudad of I; III is over the spiracle; IIIa is dorsocephalad of the spiracle; IV and V are on the same chitinization ventrad of the spiracle. Abdominal segment 8 has II only slightly below the level of I; III and IIIa are cephalad and slightly ventrad of the

spiracle. Abdominal segment 9 has setae in a line; setea II of both sides are on one dorsal chitinization; I and III are on the same chitinization below II; and V, IV, and VI are one chitinization below I and III. Setae VII is unisetose on the eighth and ninth abdominal segments, usually bisetose on the seventh. Two brown spots (probably points of attachment for muscles) are usually present, mesially, on the dorsum of the ninth abdominal segment anterior to II. Seta I was missing on both sides of the eighth and ninth abdominals and III on the left side, in the case of one larva seen.

The head is warm buff in color with large blotches of ochraceous-tawny on the sides; the sides and tips of the labrum, tips of mandibles, ocellar spot, and lateral spot at level of ocelli near posterior margin are seal brown; the adfrontal suture is pallid. In the early stages the head is uniformly fuscous black. The spinneret is well developed and strongly chitinized; the labial palpi, with terminal setae, are about as long as the spinneret. The mandibles are sharply toothed. The underside of the head is without dark pigment and lightly chitinized except at sutures. The head capsule (fig. 4) is nearly spherical, slightly flattened, a little wider than long, the greatest width well behind the middle. The incision of the dorsal hind margin is less than one-fifth of the width of the head (deeper in early stages); the distance between the dorsal extremities of the hind margin is about one-fourth the width of the head. The frons is almost twice as long as wide, nearly attaining the median incision of the hind margin; the adfrontal sutures are evenly elliptical above, sinuate below, attaining the median incision of the hind margin. The projection of the dorsal margin (as seen from the side) over the ventral is about one-fourth the diameter of the head. The ocelli are six in number; III, IV, and V are almost in a straight line; I is larger than the others; all are light in color.

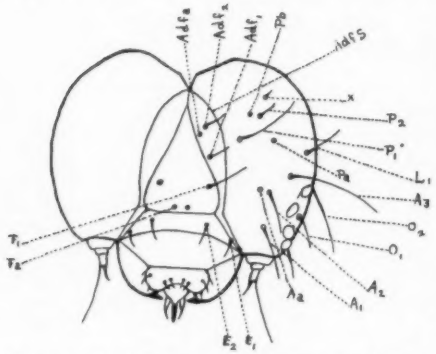

FIGURE 4.—*Grapholitha conversana*: Head capsule of mature larva. A_1, A_2, A_3, anterior setae; A_a, anterior puncture; Adf_1, Adf_2, adfrontal setae; Adf_a, adfrontal puncture; AdfS, adfrontal suture; E_1, E_2, epistomal setae; F_1, frontal seta; F_a, frontal puncture; L_1, lateral seta; O_1, O_2, ocellar setae; P_1, P_2, posterior setae; P_a, P_b, posterior punctures; x, ultraposterior puncture

The frontal punctures (F_a) lie close together considerably anterior to the setae; the adfrontal setae (Adf_1) are nearly equidistant from Adf_2 and F_1, but perceptibly nearer F_1; the adfrontal puncture Adf_a is close to Adf_2. Setae Adf_1, F_1, and E_2 are in a line. The epicranium has the normal number of primary setae and punctures. A_2, A_3, and L_1 are in a line and about equidistant; A_1 is ventrad of this line and perceptibly farther away; puncture A_a is close to and mesad of A_2, on a level with F_1 and A_2. The posterior setae and punctures, P_1, P_2, P_a, and P_b, are well above the middle of the head at about the level of the greatest width of head; P_2 is small and close to P_1, with P_b mesad of P_2 and P_a laterad of P_1, slightly dorsad of a line through P_1 and L_1.

Adf_1, P_1, and P_2 are in a line. L_1 is slightly below the level of P_1. The ocellar setae (O_1, O_2, O_3) are well separated; O_1 is closely approximate to and equidistant from ocelli II and III, O_2 is postero-ventrad of ocellus I, O_3 postero-ventrad of O_2 and about on a level with the upper margin of ocellus VI. Subocellar setae (SO_1, SO_2, SO_3) triangularly placed; SO_2 and SO_3 closer together than SO_2 and SO_1.

The full-grown larva measures approximately 7 to 8 mm. by 1.2 mm. The head capsule measures 0.77 mm. wide by 0.74 mm. long.

THE PUPA

The pupa is sayal brown in color; it is without pubescence, but with setae in about the position of those of the larva; it is about 6 mm. long by 1½ mm. wide. The fronto-clypeal suture is indistinct mesially; the eyes and glazed eyes are visible; the mandibles and clypeus are quite distinct; there are two pairs of clypeal setae, subequal, or the inner pair slightly longer than the outer; the clypeo-labral suture is distinct; the labial palpi are about one-third as long as the maxillae; the maxillary palpi extend to the proximo-lateral angles of the maxillae; the maxillae reach to approximately the level of the anterior margin of the second abdominal segment, as seen from the side, or about two-thirds of the way to the tips of the wings; the metathoracic legs and tips of the hind wings reach beyond the cephalic edge of the fourth abdominal segment, almost to the middle of that segment; the antennae extend almost to the tip of the first pair of wings, reaching to the tips of the mesothoracic legs. There is a double row of dorsal spines on abdominal segments 2 to 6 and usually at least a partial caudal row on segment 7; the spines become progressively longer from segment 2, where they are flattened and serriform, to the first row on 7, where they are long and sharp; the spines of the caudal rows are smaller than those of the cephalic rows; the rows are about equal in length except on segment 7. Segments 8 to 10, and rarely 7, have one row of spines; the spines become broader in proportion to length from 8 to 10, except that large coarse spines are alternated with smaller spines on 10. No cremaster is present. There are two fine, hooked setae on protuberant papillae on either side of the anus and a second pair just under the row of spines on the caudal margin of segment 10. The spiracles are broadly oval and produced. The anal and genital openings are slitlike, the latter single in both sexes.

FOOD PLANTS

The native host of *Grapholitha conversana* is a clover which Jepson (*3, p. 539*) has called *Trifolium involucratum* Ort., var. *fimbriatum* McDer. He gives the distribution of this variety as "wet meadows and margins of streams 4,000 to 7,500 ft.: Sierra Nevada from Tulare county to Lassen and Siskiyou Cos.; n. to B. C." The range of *T. fimbriatum* Lindl.[7] is given by Piper (*5, p. 362*) as British Columbia, Washington, Oregon, and Idaho. He listed several definite localities in eastern Washington as well as in western Washington. L. F. Henderson, curator of the herbarium of the University of Oregon, has stated (in correspondence) that he has found *T. involucratum* and its variety *T. fimbriatum* in many places in eastern Oregon, including the John Day Valley. Piper and Beattie (*6, p. 220*) state

[7] Determined by Helen M. Gilkey, Oregon State College, in 1920.

that the species *T. fimbriatum* Lindl. occurs "in wet places, especially near the seashore." It has been in the latter habitats that the writers have observed this clover and studied its severe infestation by *Grapholitha conversana*. Tidestrom (*8, p. 302*) has given the distribution of *T. fimbriatum* Lindl. as "valleys and mountain sides of the artemisia, pinyon, and yellow pine belts. British Columbia to California and Nevada." According to Jepson (*3, p. 539*), the distribution of this and other varieties of *T. involucratum*, taken together, includes practically all of the region west of the Rocky Mountains.

Red clover, *Trifolium pratense* L., when growing in the vicinity of *T. involucratum* var. *fimbriatum*, is occasionally infested by *Grapholitha conversana*, and larvae have come through to maturity on this host.

The native host resembles alsike clover, *T. hybridum* L., in some respects in its habit of growth, but alsike clover infested by *G. conversana* has not yet been observed;[8] nor has infested white clover, *T. repens* L., been found.

NATURE OF INJURY AND POSSIBLE ECONOMIC IMPORTANCE

The injury to the flower heads of *Trifolium involucratum* var. *fimbriatum* is very similar to that done to red-clover heads by the clover-seed caterpillar, *Grapholitha interstinctana*, in the Eastern States (*1, p. 134; 9, p. 15*). The larvae eat into the bases of the florets, consuming the ovules and the young seed pods, which are 2 to 6 seeded. Sometimes the larvae enter the floret from above. They pass from one floret to another, often forming tunnels, or dirty cavities, surrounded by particles of dry excrement and plant material lightly webbed together. Sometimes all the developing seed of a head is consumed. Infested heads often dry up and turn brown prematurely. In some years the loss of seed has been so heavy in places that it was found impossible to collect a respectable sample of seed. The host plant seems to be limited to certain circumscribed habitats. The degree of infestation by the seed caterpillar often varies greatly from one of these restricted localities to another. No feeding by larvae on the foliage of the plant has been observed by the writers, but such feeding is known to occur in the case of *G. interstinctana* (*1, p. 134; 9, p. 15*).

The infestations of red clover thus far observed have been very light, but it has been definitely demonstrated by the junior author, by rearing adults from red-clover heads infested by larvae, that this insect can adapt itself to that host to some extent. As the species has but one generation in a year in the coast region of Oregon, the only environment where it has been studied, injury to red-clover seed in other sections where that seed is raised might not be of any economic importance in case of an increased adaptation to that host. However, if the 1-generation cycle of this species has not become

[8] On July 12, 1929, W. E. Shull, assistant extension entomologist of the University of Idaho, sent the senior writer some specimens of lepidopterous larvae found damaging alsike clover which was being grown for seed in Idaho. These larvae were found to agree in all respects (except that they were appreciably larger) with the writers' material of *Grapholitha conversana*. However, as larvae of this subfamily often resemble one another very closely, it is not possible, in the absence of adult material, to determine the species damaging clover in Idaho. Reared moths from the same section, Idaho County, have since (in 1931) been determined as this species by Carl Heinrich.

fixed, there is a possibility of its becoming a serious pest for clover-seed growers in some parts of the region where it probably now occurs. If the species should become adapted to alsike clover it might become a serious pest even with a 1-generation cycle.

SEASONAL HISTORY

Grapholitha conversana passes the winter in the pupal state, in cocoons which are so intermingled with dried plant material and other trash as to be difficult to find. The writers have rarely collected these cocoons in their natural location in the field, but it is probable that they are concealed in the débris beneath the host plants, or occasionally even on other plants near the host, as is the case with the eastern clover-seed caterpillar (*9, p. 23*). H. K. Plank's record "from cranberry" (footnote 6) is possibly due to the formation of cocoons on plants other than the host.

Clover heads containing larvae of this species, collected on the seacoast late in June or early in July, produced moths at Forest Grove, Oreg., in the following year. Under laboratory conditions this emergence is prolonged during a period of several months. A large quantity of material, collected by the junior author June 23 and 24, 1922, at Seaside, Oreg., and kept in a moderately heated room and moistened as needed, at Forest Grove, Oreg., produced adults in 1923, as shown in Table 1.

TABLE 1.—*Emergence of adults of Grapholitha conversana under laboratory conditions at Forest Grove, Oreg., from material collected June 23 and 24, 1922, at Seaside, Oreg.*

Date of emergence	Adults emerged	Date of emergence	Adults emerged	Date of emergence	Adults emerged	Date of emergence	Adults emerged
1923	*Number*	1923	*Number*	1923	*Number*	1923	*Number*
Apr. 12	3	Apr. 30	4	May 14	2	June 3	9
Apr. 17	8	May 1	2	May 16	16	June 5	13
Apr. 20	1	May 2	2	May 18	6	June 8	6
Apr. 21	1	May 3	3	May 19	27	June 11	7
Apr. 23	2	May 4	10	May 21	19	June 14	4
Apr. 24	1	May 5	13	May 23	7	June 18	2
Apr. 25	9	May 7	12	May 25	7	June 21	0
Apr. 26	3	May 9	23	May 27	6	July 7	[a] 1
Apr. 27	7	May 11	3	May 29	11	July 9	1
Apr. 28	4	May 12	12	May 31	1	July 11	0

[a] Recently emerged, active, fresh, unrubbed.

These records show that the maximum emergence took place in May, but that the whole period of emergence covered three months. The last emergence occurred more than a year after the date of collection. Field observations have indicated that a similar prolonged period of emergence occurs under natural conditions, as eggs and young larvae have been found late in June and moths were collected in the field at Seaside, Oreg., on June 25, 1923. However, emergence in the cool climate of the seacoast region of Oregon and Washington probably does not occur as early as April, for the junior writer was unable to find any stages of this insect at Seaside on May 8, 1924. According to Kearfott (*4, p. 61*), A. H. Vachell collected moths in large numbers at San Luis Obispo, Calif., in March, and at Carmel, Calif., in April. On June 1, 1928, the junior writer found many

moths flying about *Trifolium involucratum* var. *fimbriatum* and red clover at Seaside. However, at the same time she also collected many larvae, a few of which were nearly full grown—an indication that some moths had been present some weeks earlier. On May 12, 1930, in the same locality, she found hundreds of freshly emerged adults flying about the host plants, but could find no eggs.

The moths fly to the host plants late in the afternoon or early in the evening. The eggs are deposited on the underside of the involucre or around the bases of the flower heads. These blisterlike eggs are usually laid singly, but may be laid in small batches, as is illustrated in Figure 5. The junior author found eggs in abundance at Seaside, Oreg., on June 1, 1928. Some fresh eggs hatched in 12 days (some were still unhatched on June 13) at room temperatures.

FIGURE 5.—Eggs of *Grapholitha conversana* on host plant

A few larvae which were collected as nearly mature on June 1, 1928, spun their cocoons on June 13. However, in the field well-grown larvae are not found in numbers until late in June and in July. The earliest record for a pupa taken in the field was June 24, 1926, at Seaside. Laboratory material has pupated as late as September.

These seasonal notes show that *Grapholitha conversana* has but one generation in a year in the coastal region of Oregon. Whether or not this 1-generation life cycle is fixed for the species is not known, as the insect has not been studied in habitats where the moths emerge considerably earlier than they do on the Oregon coast.

NATURAL ENEMIES

From *Grapholitha conversana* two species of hymenopterous parasites have been reared—*Orgilus mellipes* (Say),[9] emerging on July 26, 1920, and July 22, 1922, from material collected July 12, 1920, and June 23, 1922, respectively, and *Microbracon hyslopi* Vier.,[9] emerging August 10 1920, from material collected July 12, 1920.

SUMMARY

There is a possibility that some of the insects attacking the native leguminous flora of the North Pacific region may become pests of cultivated forage crops.

Grapholitha conversana Wlsm. is a caterpillar attacking the seed of a native clover, *Trifolium involucratum* var. *fimbriatum*, on the seacoast of Oregon. This insect has been recorded also from eastern Oregon and the California coast. The distribution of its native food plant suggests that it may occur in other localities west of the Rocky Mountains.

The larvae attack the flower heads of *T. involucratum* var. *fimbriatum*, and, occasionally, red clover, *T. pratense*, growing in proximity to the native host. In the case of the native host the ovules and young seed pods are consumed with considerable loss in seed production. No clover-seed caterpillar has been known heretofore in the

[9] Determined by A. B. Gahan.

North Pacific region. It is possible that, under certain conditions, this species might become a serious pest of cultivated clovers.

Two species of parasites of the hymenopterous family Braconidae have been reared from *Grapholitha conversana*.

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INFLUENCE OF THALLIUM SALTS UPON THE MOLTING MECHANISM OF FOWLS [1]

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INTRODUCTION

Within the last few years a considerable number of reports dealing with the effect of feeding different thyroid preparations and thyroxin upon the molting mechanism of chickens have been published. In all these experiments it was found that the feeding of thyroid substance or of thyroxin not only caused the birds to molt but also that it influenced the shape and pigmentation of the feathers which regenerate in such experimentally induced molting. These results led some investigators to the conclusion that under normal physiological conditions the thyroid controls the mechanism of molting and that it also plays an important rôle in the process of pigment deposition.

A series of experiments was designed to determine whether or not it is justifiable to attribute to the thyroid a specific action of this type. The first experiments of the series were concerned with the influence of thallium salts, chiefly thallium acetate, on the molting of fowls. This report presents the results of these experiments.

Experiments with thallium were suggested by the interesting effects of thallium on the hair covering of rodents observed by Buschke and Peiser. Buschke and Peiser [2] based their experiments on the fact, known for some time previously, that thallium poisoning or oral administration of thallium in minute quantities will in time cause an almost complete loss of the hair of head and body in human beings. When Buschke and Peiser fed rats and mice with thallium acetate they found that the animals soon began to shed their hair. Usually the hair in the region of the head and back fell out first, while that on the ventral side of the body resisted the depilatory action of the thallium longer than did that on any other part of the body. Similarly, after the treatment was discontinued the hair first came back on the ventral side and last in those regions (head and dorsum) from which it had first been shed. A long and carefully dosed treatment led to complete loss of all hairs except the vibrissae, which are always retained. Only young animals, however, showed an extreme response to thallium by a complete loss of the body covering. Definite individual differences were observed in the degree to which shedding took place. Complete reviews of the work concerning the influence of thallium upon hair growth have been given by Truffi [3] and by Munch and Silver.[4]

[1] Received for publication Feb. 2, 1931; issued July, 1931.

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EXPERIMENTAL DATA

The writer began some preliminary experiments with chickens in July, 1929. Two cockerels and two pullets were given each a daily dose of 50 c. c. of 0.04 per cent solution of thallium acetate in water with their mash. After four or five days the birds did not consume all the mash, and from then on the daily dose was introduced directly into the proventriculus by means of a catheter and bulb. About seven days after the first treatment all the birds had diarrhea, the droppings showing the intense green color that appears to be typical of thallium poisoning. By about the ninth day the birds had completely lost control of their muscles; their wings were hanging down and they were unable to stand. About two days later they died.

FIGURE 1.—Silver Spangled Hamburg ♂ No. 1 at the beginning of the experiment

Another chicken was given a daily dose of 10 mgm. of thallium acetate in water by subcutaneous injection. This treatment was followed by the same symptoms which were observed after oral administration; only, corresponding to the lower dose, the poisoning became manifest somewhat later and the bird died 19 days after the treatment was started. The birds which had been treated per os began to lose feathers shortly before death.

FIGURE 2.—Silver Spangled Hamburg ♂ No. 1 after eight weeks of treatment with thallium acetate (September 24, 1929). Extreme loss of feathers from throat and breast

A new experiment was begun August 1, 1929. Sixteen birds were used in this group, nine cockerels and seven pullets. They were between 4 and 5 months old. Two cockerels and two pullets were of purebred Silver Spangled Hamburg stock; the rest had a crossbred ancestry. There were two barred cockerels and two barred pullets, two cockerels and two pullets with white plumage, and a few small black flecks (heterozygous dominant white), and one black pullet and three black cockerels (of the last-mentioned one, at the beginning of the experiment was erroneously classified as a pullet). All of these birds received 25 c. c. of a solution of 0.1 gm. thallium acetate in 1 liter of water every second day. On October 12 the strength of the solution was increased to 0.15 gm. per liter and on November

5 to 0.2 gm. per liter. Throughout the experiment the thallium solution was introduced directly into the proventriculus with a catheter and bulb. When any bird began to show symptoms of poisoning the treatment was interrupted until the bird again appeared normal.

Treatment with small doses of thallium acetate causes, after a certain time, in both males and females a diffuse shedding of feathers in different regions of the body. This loss of feathers is most pronounced on throat, neck, breast, and head; in other regions only a few feathers are shed. New feathers grow out at once in place of those which have been shed. In females this molt comes to an end after a certain time, and from then on the thallium treatment remains ineffective as far as the plumage is concerned. In males, on the other hand, the initially diffuse molting leads to an extreme loss of feathers from the lower part of the throat and from the upper part of the breast (figs. 1–4), and sometimes also from the neck. These areas eventually become entirely bare and remain so for a considerable length of time. Finally, new feathers begin to grow out again on these places, and, at the same time, the thallium gradually loses its specific action on the molting mechanism. This sexual difference in response to thallium was particularly striking in the black cockerel which, because of sexual immaturity, was classified as a pullet at the beginning of the experiment. About two and one half months after the experiment began, all eight other males showed distinct bare spots on the throat, but this individual in appearance and plumage reaction still resembled a pullet. Some time later, however, when sudden growth of the comb took place, the bird was recognized as a cockerel, and still later he developed a bare area in the typical manner.

FIGURE 3.—Black ♂ No. 1 after 11 weeks of treatment with thallium acetate. Large bare spot on throat and breast

A large number of pullets and cockerels belonging to the families from which the treated birds had been chosen were kept throughout the duration of the experiments. In none of these control birds did a shedding of feathers occur similar to that observed in the thallium-treated individuals. The bare areas which developed on throat and breast of cockerels as a consequence of continued thallium adminis-

tration did not resemble the condition produced by ordinary neck and breast molt.

Two of the thallium-treated cockerels were mated to normal Leghorn pullets and gave excellent fertility. Some of the thallium-treated pullets laid at infrequent intervals.

Other thallium compounds were tested for their effect on plumage. Although the response of the chickens in general appeared to be the same as to thallium acetate, in none of the tests was there an equally extreme loss of feathers. The approximate order of the thallium salts tested, according to their influence on the plumage, was as follows: (1) Acetate, (2) fluoride, (3) sulphate, and (4) carbonate.

FIGURE 4.—Black ♂ No. 2 after 14 weeks of treatment with thallium acetate. Large bare spot on throat and breast

Buschke and others found that young rodents show a more extreme response to thallium treatment than do older ones. To determine whether the same were also true of chickens an experiment was made in which 13 chicks were treated with thallium on the second day after hatching, and 14 chicks of the same hatch were kept for controls. Treatment was started with a dose of 2 c. c. of a solution of 0.025 gm. thallium acetate in 1 liter of water, which was introduced directly into the proventriculus. Treatment was repeated every second day and the dosage was rapidly increased with the growth of the chicks, until by the time they were 7 weeks old it had been brought up to 15 c. c. of a solution of 0.4 gm. thallium acetate in 1 liter of water. One week later it was necessary to interrupt the treatment for 10 days. It was then resumed with about the same dose. Most of the chicks died from chronic poisoning at 10 to 11 weeks of age. No significant influence of the thallium treatment could be discovered in the plumage of any one of the chicks. On the basis of the amount of thallium given per unit of body weight it is clear from this experiment that the lethal dose of thallium is many times larger for young than for mature chickens.

Finally, it is necessary to consider whether the thallium treatment had any influence upon the color, pattern, and shape of the feathers which were regenerated in the course of molting induced by thallium treatment. The most critical evidence on this point seems to be that furnished by the plumage regenerated on the bare areas which had appeared in all thallium-treated cockerels. All feathers which grew out on these places proved to be entirely normal with regard to color, pattern, and shape. In the four birds which were heterozygous for dominant white a very slight increase in the number of feathers with black spots could be observed in the course of the experiment.

This can not be considered significant. In some of the birds it was found that a part of the regenerating feathers kept the feather sheath for a considerable length of time. (Fig. 5.) This was observed in both males and females and in all regions of the body.

Although the regeneration of feathers appears to be somewhat retarded in molting induced by thallium treatment, while in molts induced by thyroid administration the replacement of feathers appears to be accelerated, and although no irregularities in the pigmentation of the feathers similar to those obtained in the thyroid experiments have been observed, the experiments do not eliminate the possibility that the observed effects of thallium salts may themselves be due to

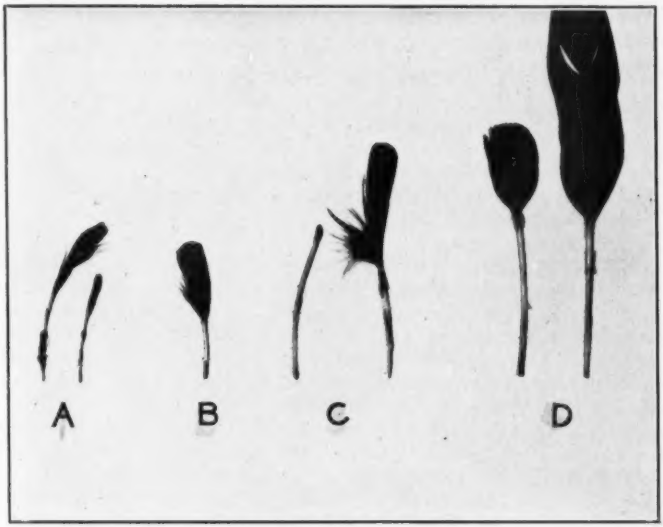

FIGURE 5.—Feathers from black ♀ 8619, regenerated during a molt induced by thallium acetate treatment, the sheaths of the feathers have been retained for an abnormally long time: A, Neck; B, breast; C, saddle; D, tail feathers

an effect of these substances on the thyroid gland. As a matter of fact, nothing definite is known concerning the mechanism by which thallium acts upon the skin and its derivatives.

CONCLUSIONS

From experiments in which young chicks and mature cockerels and pullets were treated with thallium salts the following conclusions are drawn:

Treatment of mature cockerels and pullets with thallium acetate is followed by a diffuse loss of feathers. More feathers are shed from the region of throat, breast, neck, and head than from the rest of the body. New feathers grow out at once in place of those that have been shed.

In females this diffuse molting gradually becomes less pronounced and the thallium ceases to have an effect on the plumage. In males, however, large bare areas appear on the lower part of the throat and

upper part of the breast, and sometimes extend to the neck. Regeneration of feathers on these regions takes place after a time, and simultaneously the thallium becomes ineffective as far as the body plumage is concerned. This sexual difference was observed in all of the 16 birds used in the experiment.

The feathers which regenerate during molting induced by thallium are normal with regard to color, pattern, and shape. In some instances it was observed that such feathers stay in their sheath for an abnormally long time.

Of the different thallium salts which were tested (acetate, fluoride, sulphate, carbonate), the acetate proved to have the most pronounced, and carbonate the least pronounced, effect on the plumage.

Young chicks were found to be much more resistant to thallium poisoning than older birds and their plumage showed no effect of the thallium treatment.

AN INSTRUMENT FOR DETERMINING THE BREAKING STRENGTH OF STRAW, AND A PRELIMINARY REPORT ON THE RELATION BETWEEN BREAKING STRENGTH AND LODGING[1]

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INTRODUCTION

Lodging has long been recognized as an important factor in growing small grains. In recent years its importance has been greatly increased by the advent of the combine and the necessity of often permitting the grain to stand after it is ripe. In choosing varieties and in developing new ones it is therefore necessary to give more consideration than usual to this tendency to lodge.

Without attempting a critical discussion of lodging and its causes, it may be pointed out that the degree varies greatly from season to season and from farm to farm according to rainfall, wind, fertility of the soil, stand, rapidity of growth, stage of growth at which conditions favorable to lodging occur, and probably to other factors as well. It has frequently been observed of all varieties that they may lodge completely or not at all. Moreover, it is impossible to determine which varieties will lodge under a given set of conditions. Sometimes varieties with a well-earned reputation for resistance to lodging lodge more than susceptible varieties because of the stage of development that they happen to be in when conditions are favorable for lodging. These facts make it highly desirable that some simple means of determining relative tendencies to lodge be devised.

The breaking strength of the straw would seem to offer possibilities in this direction. In fact, Albrecht (*1*)[2], as noted by Garber and Olson (*3*), accepted a relation between breaking strength and lodging without question, and Helmick (*4*) has shown that Turkey wheat, which is noted for its tendency to lodge, has but little more than half the breaking strength of Red Wave, a soft wheat known to be resistant to lodging. Gainey and Sewell (*2*), using the instrument herein described, determined the breaking strength of the straw from 22 pairs of wheat plats from as many fields. One plot of each pair had more available nitrogen than the other. The average breaking strength of the straw on the plots having the most nitrogen was found to be 37.5 per cent greater.

Helmick (*4*) and Willis (*7*) have each devised an apparatus for determining breaking strength of straw. Recently Tubbs (*6*) has studied the relation between manurial deficiency and mechanical strength of barley straw, the latter being measured by the force required to crush portions of the straw. This by no means exhausts the literature relating to lodging and its causes, nor has mention been made of all attempts to devise means for determining breaking strength. A critical review of the subject is not intended at the present time. Instead it is proposed to report an attempt to devise

[1] Received for publication Dec. 17, 1930; issued July, 1931. Contribution No. 200, Department of Agronomy, Kansas Agricultural Experiment Station.

[2] Reference is made by number (italic) to Literature Cited, p. 82.

a simple apparatus by means of which breaking strength may easily, quickly, and accurately be determined and to present a report of certain results that have been secured with it. The instrument has been used at the Kansas Agricultural Experiment Station in five different seasons, and Leidigh, Mangelsdorf, and Dunkle (*5*) have recently reported results obtained with it in two years' work, at the Texas station.

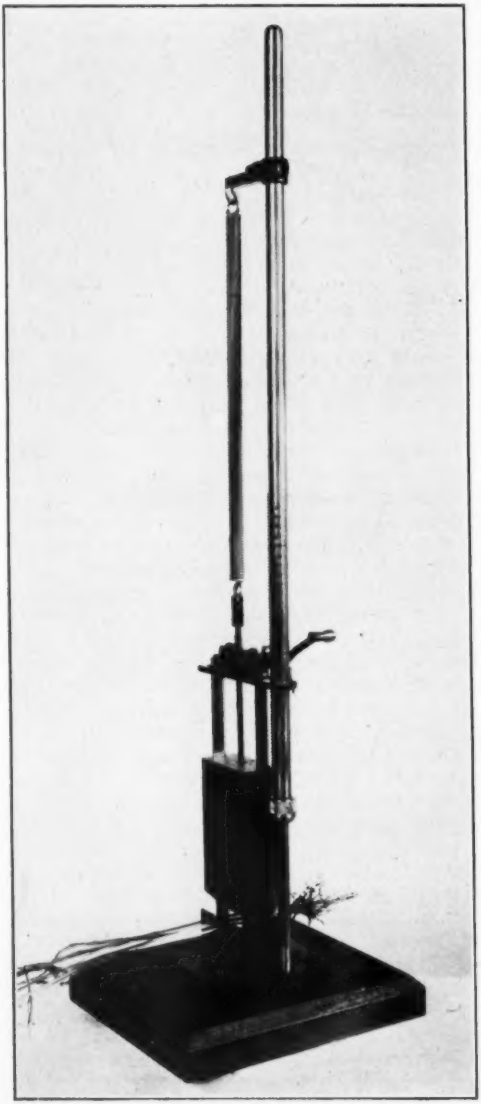

FIGURE 1.—Instrument for determining the breaking strength of straw

THE INSTRUMENT

The instrument (fig. 1) consists essentially of a brass weight beveled and bluntly pointed at the lower end, capable of being raised between standards or guides, the latter fitting into grooves on the sides of the weight. The weight is supported by a coil spring, which in turn is attached to a vertically movable support. The straws to be broken are supported on crosspieces 2 inches apart (inside measurement) so placed that when the weight is lowered it rests on the straws exactly halfway between the supports. The movable support to which the spring and weight are attached is provided with a ratchet in which a ratchet wheel operates and by means of which the support and the weight attached to it are raised and lowered. The position of the support at any time may be recorded by means of a graduated scale and a pointer, the latter being on the stationary part of the machine.

As the support is lowered, more and more of the weight is permitted to rest on the straws and less of it is supported by the spring. With the gradual lowering of the weight, a point is reached at which the straws break. This point is recorded by means of previous calibrations expressed as pounds. Several straws may be broken at one time, the number depending on the weight and on the space provided for them on the supports. In the first three years' experiments reported here, 5 straws were broken at a time; in the last two years 10 have been broken at one time.

METHODS

In certain instances, determinations were made at various stages of growth, but those for the mature culm seemed to afford the most reliable comparison of varietal characteristics, and the data presented herein are without exception from mature culms taken at harvest and hung up under shelter to cure for approximately a month. The culms were chosen at random from the plot, except that those from nearr the borders or near skips or blank spaces in the plots were not taken.

Determinations have also been made at various points on the culm. In general the comparative results appeared to be about the same regardless of the exact location, provided only that it was the same for all varieties. In the work reported here the culms were broken in the first internode above the ground that were of sufficient length (2 inches) to reach across the supports of the instrument.

Two persons usually operate the instrument, one arranging the straws in place and the other lowering the weight and recording the results. The straws are placed with the lower node of the internode to be broken on one of the supports. In this way all straws are broken at a uniform distance (1 inch) above the node.

The random method of selection results, of course, in securing culms of different sizes in each sample. It might be supposed that when the weight is lowered it would be supported by the larger culms and that the breaking strength would then depend on the larger culms alone and be different from what it would be were each culm broken separately. This may to a slight extent be true. It should be remembered, however, that the culms are somewhat flexible so that near the breaking point the weight is being supported by all culms of the sample. Hence, it seems not unreasonable to suppose that the results presented here are substantially the same as though the culms had been broken one at a time. The instrument could be adapted to break single culms, but the labor in making the determinations would of course be greatly increased.

The breaking determinations as made in the manner here described are rapid and appear to be very accurate. Although there has seemed to be no practical method of distinguishing accurately between the two kinds of errors, it appears that errors in sampling—that is, in securing straws for breaking—are considerably greater than those inherent in the manipulation of the instrument.

The breaking strength of the straw of a considerable number of varieties grown in field plots and in some cases in the cereal crop nursery at Manhattan have been determined during the last five years. The degree of lodging has been recorded in each case where lodging occurred, and this information is available also for certain years before breaking-strength determinations were undertaken.

Lodging has been estimated on a percentage basis, taking into consideration both the proportional part of the plot which was lodged and also the degree or severity of the lodging. Often the lodging was estimated two or more times during the season, as for example when slight lodging was increased to severe lodging by wind or rain. In the tables which follow, the data given are for the date on which most lodging was recorded.

Strength of straw determinations were first made in 1926, the determinations being for varieties grown in field plots. These were repeated in 1927, 1928, 1929, and 1930. In 1928, 41 varieties and strains from the cereal crop nursery, ranging in degree of lodging from 0 to 90 per cent, were chosen for a special study of this relation.

EXPERIMENTAL DATA

Tables 1–6 give the percentage of lodging except for 1926 and 1930, when no lodging of importance occurred, and the breaking strength of the straw for the varieties grown in replicated field plots in 1926 to 1930, and for the 41 strains from the cereal crop nursery in 1928. The number of culms per acre at harvest (determined by counting the number in a 5-foot segment of a drill row in from three to five places in each plot) are also included, since, as will appear later, stand appears to be related to lodging and to breaking strength. More extensive data pertaining to certain well-known varieties, together with data relating to breaking strength of the straw so far as available, are given in Table 7. Gross and partial correlations between breaking strength and lodging, breaking strength and stand, and between lodging and stand are given in Table 8. The figures in the tables are for the most part averages for three plots. Those pertaining to breaking strength of straw are averages of 10 determinations from each plot. The varieties are arranged in order of the breaking strength of the straw.

TABLE 1.—*Breaking strength of straw and culms per acre of winter wheat varieties at harvest in 1926*

Variety	Accession record No.[a]	Culms per acre at harvest (000 omitted)	Breaking strength of straw in pounds per straw
Shepherd	6,163	1,798	1.46±0.037
Harvest Queen	6,199	2,274	1.25± .025
Hussar	4,843	1,919	1.10± .027
Currell	3,326	2,231	1.10± .021
P 1068×Marquis	Kans. 442	2,074	1.04± .021
Fulcaster	6,471	2,689	1.03± .021
Zimmerman	6,211	2,150	.96± .017
Kawvale	6,274	2,394	.92± .024
Blackhull	6,251	2,271	.92± .023
Iobred	6,934	2,386	.92± .021
Nebraska No. 28	5,147	2,016	.91± .012
Renmarq	6,936	2,321	.90± .024
Nebraska No. 6	6,249	2,379	.89± .015
Sherman	4,430	2,324	.87± .005
Marquis×Kanred	Kans. 443	2,643	.87± .013
Superhard	8,054	1,914	.86± .008
Kanmarq	6,937	3,129	.84± .023
Kharkof	6,206	2,322	.84± .015
Newturk	6,935	2,559	.79± .018
Altara	5,797	2,626	.78± .020
Turkey	1,558	2,819	.75± .014
Improved Turkey	5,592	2,679	.74± .037
Kanred	5,146	2,150	.73± .018
P 1068 selection	Kans. 2,658	2,330	.72± .011
Regal	7,364	2,588	.71± .005
Hard Winter Defiance	6,205	3,096	.70± .025

[a] Accession record number of the Division of Cereal Crops and Diseases, U. S. Department of Agriculture, except as otherwise indicated as Kansas accession record number.

TABLE 2.—*Breaking strength of straw, lodging, and culms per acre of winter wheat varieties at harvest in 1927*

Variety	Accession Record No. [a]	Culms per acre at harvest (000 omitted)	Breaking strength of straw in pounds per straw	Lodging
				Per cent
Hussar	4843	2,489	1.08±0.009	2.0
Harvest Queen	6199	2,841	1.09± .008	.7
Shepherd	6163	2,404	1.08± .007	3.5
Iobred	6934	2,848	1.06± .009	2.0
Sherman	4430	2,629	1.02± .007	3.3
Kawvale	5274	2,853	1.00± .008	10.0
Fulcaster	6471	2,972	1.00± .007	8.3
Tenmarq	6936	2,698	.99± .008	9.3
Nebraska No. 6	6249	2,692	.99± .008	.3
Turkey	1558	2,488	.97± .006	.7
Currell	3326	2,865	.95± .008	.3
Turkey	5592	2,769	.93± .006	1.7
P 1066×Marquis	Kans. 442	2,794	.92± .006	5.3
Altara	5797	2,803	.90± .006	.3
Kharkof	6205	2,388	.90± .005	1.3
Superhard	8054	2,758	.90± .007	16.7
Blackhull	6251	2,665	.89± .006	14.7
Marquis×Kanred	Kans. 443	3,241	.88± .006	8.7
Hard Winter Defiance	6205	2,871	.85± .006	.0
Kanmarq	6937	3,163	.84± .006	11.7
Newturk	6935	3,063	.84± .006	0
Zimmerman	6211	2,852	.84± .006	0
Regal	7364	2,615	.82± .007	0
P 1068 selection	Kans. 2658	2,906	.82± .008	17.7
Nebraska No. 28	5147	2,607	.81± .007	4.3
Fulhard	8257	2,822	.80± .011	0
Kanred	5146	3,085	.79± .004	13.3
Early Kanred	Kans. 2521	2,549	.62± .011	15.0

[a] See note *a*, Table 1.

TABLE 3.—*Lodging, breaking strength of straw, and culms per acre of winter wheat varieties at harvest in 1928*

Variety	Accession Record No. [a]	Culms per acre at harvest (000 omitted)	Breaking strength of straw in pounds per straw	Lodging
				Per cent
Harvest Queen	6199	2,203	0.99±0.032	0
Fulcaster	6471	1,984	.94± .040	0
Currell	3326	2,074	.89± .009	0
Michigan Wonder	Kans. 500	2,077	.89± .023	0
Kawvale	8180	2,276	.87± .025	0
Hussar	4843	2,122	.83± .036	11.7
Early Blackhull	8856	2,628	.79± .030	6.5
Blackhull	6251	2,739	.77± .009	7.0
Fulhard	8257	2,522	.77± .002	0
Early Kanred	Kans. 2521	2,981	.76± .008	0
Tenmarq	6936	2,468	.78± .036	6.0
Marquis×Kanred	Kans. 443	2,772	.75± .017	4.0
Superhard	8054	2,540	.73± .026	8.7
Menno	Kans. 496	2,517	.71± .015	0
Nebraska No. 6	6249	2,593	.70± .017	6.7
Kanmarq	6937	2,642	.70± .020	1.7
Red Hull	Kans. 487	2,591	.69± .059	5.0
P 1068×Marquis	Kans. 442	2,490	.68± .022	14.3
Kharkof	2193	2,568	.68± .010	3.7
Newturk	6935	2,997	.66± .005	3.7
Oro	8220	2,926	.66± .021	3.3
Kanred	5146	2,884	.64± .007	17.3
Regal	7364	3,068	.64± .027	3.3
Turkey	1558	2,673	.64± .097	3.7

[a] See note *a*, Table 1.

TABLE 4.—*Lodging, breaking strength of straw, and culms per acre of winter wheat varieties at harvest in 1929*

Variety	Accession Record No. [a]	Culms per acre at harvest (000 omitted)	Breaking strength of straw in pounds per straw	Lodging
				Per cent
Harvest Queen	6199	2,244	0.81±0.007	28.3
Fulcaster	6471	2,314	.75± .020	50.0
Currell	3326	2,125	.74± .014	21.7
Michigan Wonder	Kans. 500	2,299	.69± .018	60.0
Fulhard	8257	2,778	.65± .012	61.7
Kawvale	8180	2,309	.63± .045	26.7
Tenmarq selection	Kans. 2637	2,439	.63± .022	61.7
Kanred×Hard Federation	Kans. 2627	2,399	.62± .020	6.7
Early Blackhull	8856	2,060	.62± .009	53.3
Tenmarq	6936	2,434	.61± .024	55.0
Prelude×Kanred	8886	2,021	.60± .024	70.0
Kanred×Marquis	Kans. 2644	2,633	.57± .016	55.0
Kanred×Hard Federation	Kans. 2648	2,379	.57± .007	58.3
Red Hull	Kans. 487	3,136	.57± .014	75.0
Blackhull	6251	2,653	.57± .012	76.7
Oro	8220	2,638	.56± .028	15.0
Kharkof	2193	2,559	.56± .011	78.3
Kanred×Marquis	Kans. 2638	2,703	.55± .000	71.7
Turkey	1558	2,738	.54± .014	83.3
Kharkof (Hays No. 2)	6686	2,828	.51± .014	68.3
Superhard	8054	2,588	.50± .010	84.2
Kanred	5146	2,693	.50± .010	84.2
Newturk	6935	3,778	.48± .012	98.3

[a] See note *a*, Table 1.

TABLE 5.—*Breaking strength of straw of winter wheat varieties and culms per acre at harvest in 1930*

Variety	Accession Record No.[a]	Culms per acre at harvest (000 omitted)	Breaking strength of straw in pounds per straw
Currel	3326	1,913	1.28±0.107
Harvest Queen	6199	2,031	1.16± .157
Fulcaster	6471	2,255	1.06± .128
Michigan Wonder	Kans. 500	2,051	.95± .015
Nebraska No. 50	8885	2,180	.90± .038
Fulhard	8257	2,101	.89± .032
Prelude×Kanred	8886	1,667	.88± .030
Kawvale	8180	2,110	.88± .017
Cooperatorka	8861	2,295	.85± .052
Kharkof (Hays No. 2)	6686	2,205	.84± .028
Tenmarq selection	Kans. 513	1,961	.83± .032
Tenmarq selection	Kans. 2637	2,036	.81± .018
Oro	8220	2,225	.79± .034
Kharkof	2193	2,174	.78± .024
Blackhull	6251	2,339	.78± .015
Turkey	1558	2,354	.78± .012
Tenmarq	6936	2,250	.75± .022
Superhard	8054	2,414	.75± .021
Kanred×Marquis	Kans. 2642	2,389	.73± .017
Kanred	5146	2,389	.72± .009
Tenmarq selection	Kans. 514	2,145	.72± .008
Kanred×Marquis	Kans. 2640	2,245	.72± .024
Kanred×Marquis	Kans. 2644	2,494	.72± .010
Kanred×Hard Federation	Kans. 2627	1,991	.70± .009
Kanred×Marquis	Kans. 2647	2,105	.70± .003
Prelude×Kanred	Kans. 2652	1,802	.69± .010
Early Blackhull	8856	1,842	.66± .013
Nebraska 28	5147	2,016	.66± .015

[a] See note *a*, Table 1.

TABLE 6.—*Lodging and breaking strength of straw of winter wheat grown in cereal crop nursery, 1928*

Variety	Kansa selection No. or Kansas accession record No.	Breaking strength of straw in pounds per straw	Lodging	
			June 6	June 14
			Per cent	*Per cent*
Kanred×Hard Federation	255007	0.79±0.026	0	0
Illini Chief×Marquis	242212	.74± .031	0	0
Tenmarq	Kans. 439	.70± .016	0	15
Kanmarq	Kans. 440	.65± .021	0	5
Illini Chief × Marquis	223421	.65± .015	0	0
Do	242216	.64± .022	0	0
Do	242234	.64± .017	0	0
Kanred×Hard Federation	254887	.63± .023	0	0
Tanmarq selection	264308	.63± .021	2	26
Kanred×Hard Federation	255107	.62± .013	0	0
Do	255005	.62± .023	0	0
Do	243518	.62± .015	0	5
Do	254909	.61± .014	0	3
Tenmarq selection	Kans. 2637	.61± .015	0	5
Kanred×Hard Federation	254990	.60± .015	0	10
Illini Chief×Marquis	242217	.59± .018	0	0
Kanred×Hard Federation	254976	.59± .009	0	0
Tenmarq selection	264306	.57± .011	4	35
Kanred×Hard Federation	243181	.56± .023	0	0
Fulhard	Kans. 2594	.55± .015	0	40
Kanred×Hard Federation	255030	.54± .013	0	0
Do	254890	.52± .014	0	5
Superhard	Kans. 470	.52± .014	5	20
Kanred×Hard Federation	243571	.51± .014	35	70
Kawvale	Kans. 2593	.50± .006	10	25
Kanred×Hard Federation	255080	.49± .009	0	0
Blackhull	checks	.49± .010	17	35
Kanred×Hard Federation	254996	.49± .011	0	0
Do	255046	.49± .008	0	10
Do	254545	.49± .010	0	0
Do	255085	.48± .010	10	35
Do	254991	.48± .012	15	25
Do	Kans. 2648	.48± .014	50	90
Do	Kans. 2651	.48± .010	5	0
Illini Chief selection	223415	.47± .011	0	0
Kanred	checks	.45± .007	38	83
Kanred×Hard Federation	254902	.45± .008	0	0
Menno	Kans. 496	.44± .010	40	85
Kanred×Hard Federation	Kans. 2649	.42± .012	20	75
Do	Kans. 2625	.42± .008	70	85
Do	Kans. 2626	.40± .012	15	75

TABLE 7.—*Lodging and breaking strength of straw of certain winter wheat varieties grown in field plots and in the cereal crop nursery*

Variety	Percentage of lodging in field plots in year indicated					Percentage of lodging in cereal crop nursery in year indicated							Average percentage of lodging (12 observations)	Difference in percentage of lodging compared with Harvest Queen (plus (+) or minus (−))	Average breaking strength of straw, 1926 to 1930
	1919	1923	1927	1928	1929	1919	1923	1925	1926	1927	1928	1929			
Harvest Queen	42.0	2.0	0.6	0	28.3	10.6	80.0	0	0	77.4	3.2	54.0	24.8	0	1.06
Fulcaster	----	0	8.3	0	50.0	25.0	100.0	39.3	----	72.4	13.2	82.0	----	13.5	.96
Kawvale	----	----	10.0	0	25.7	----	65.0	40.0	0	72.5	37.2	43.0	----	5.7	.86
Nebraska No. 6	75.0	26.7	.3	6.7	----	33.3	90.0	60.0	0	59.3	25.7	----	----	16.1	[a].86
Tenmarq	----	----	9.3	6.0	55.6	----	70.0	50.0	5.0	69.1	44.0	81.0	----	13.1	.80
Blackhull	67.0	6.7	14.7	7.0	76.7	26.7	95.0	10.0	0	76.6	45.6	83.0	39.7	17.5	.79
Kharkof	93.0	25.0	1.3	3.7	78.3	41.6	90.0	80.0	0	73.3	22.5	78.6	45.3	24.1	.75
Turkey	96.0	10.0	.7	2.7	83.3	11.3	90.0	85.0	6.7	79.9	24.4	84.0	44.9	23.1	.73
Kanred	99.0	44.5	13.3	17.3	84.2	26.0	95.0	70.6	.7	76.4	64.8	89.0	56.6	31.9	.68

[a] Arrange for 4 years only. The average for Kanred in the same year was 0.72.

TABLE 8.—*Correlations between breaking strength of straw, lodging, and stand of winter wheat varieties at Manhattan, Kans., in 1927, 1928, and 1929*

Year	Number of tests	Breaking strength and lodging		Breaking strength and stand		Lodging and stand	
		Gross correlation r_{12}	Partial correlation stand constant $r_{12.3}$	Gross correlation r_{13}	Partial correlation lodging constant $r_{13.2}$	Gross correlation r_{23}	Partial correlation breaking strength constant $r_{23.1}$
1926	26			−0.631±0.094			
1927	28	−0.310±0.085	−0.277±0.118	−.200± .103	−0.139±0.116	+0.228±0.121	+0.178±0.123
1928	24	−.416± .114	−.404± .115	−.800± .050	−.861± .050	+.225± .131	−.198± .132
1929	23	−.583± .063	−.361± .122	−.552± .098	−.380± .120	+.483± .108	+.238± .133
1930	28			−.225± .124			

1=breaking strength, 2=lodging, 3=stand.

Probably the best evidence of a relation between breaking strength and lodging is the fact that in all tables the soft wheats which are noted for resistance to lodging are grouped near the top, while the hard wheats which lodge easily are invariably near the bottom. Varieties believed to be intermediate in this respect, such as Blackhull, Superhard, Nebraska No. 6, Oro, and Tenmarq, without exception occupy an intermediate position with respect to breaking strength.

The gross and partial correlations presented in Table 8 do not completely support this view. This is probably due in part to the fact that lodging is a very complex phenomenon, depending not only on breaking strength of the culm but also on length of the culms, amount of grain produced per head, and especially the particular stage of growth of the plant when storms causing lodging occur. These tend to obscure whatever relation there may be between breaking strength and lodging.

In the case of the varieties from the cereal crop nursery, the data of which appear in Table 6, the relation is clearly nonlinear. The number is scarcely sufficient to justify the calculation of a correlation ratio, and hence no statistical measure of relationship is attempted in this case. It is of course possible, if not probable, that the relation is not strictly linear in other cases, but here also the number involved is not sufficient to justify critical tests for linearity. It is not likely that whatever departure from linearity there may be is sufficient to alter in any material way the interpretation of the results given above.

It is of special interest to determine to what extent observations with respect to lodging and to breaking strength of straw in any year or series of years may be used to predict behavior with respect to these characteristics in future years. For this purpose the correlation between lodging in each year and that for every other year in which lodging occurred has been calculated, and the same has been done with respect to breaking strength of the straw. The data are presented in Tables 9 and 10.

TABLE 9.—*Interannual correlations between lodging of winter wheat varieties*

Year	1927	1928
1928	0.224±0.146	
1929	.144± .190	0.519±0.121

TABLE 10.—*Interannual correlations between breaking strength of straw of winter wheat varieties*

Year	1926	1927	1928	1929
1927	0.679±0.074			
1928	.845± .045	0.512±0.113		
1929	.937± .025	.667± .018	0.922±0.026	
1930	.826± .063	.596± .115	.777± .062	0.789±0.052

It will be noted that whereas the correlations between lodging in various seasons are low and in two cases of the three are not statistically significant, those between breaking strength in different seasons are medium to high, and in all cases are highly significant. The fact that the correlations shown in Table 9 are even less than the gross correlations between breaking strength and lodging as shown in Table 8, taken in connection with the high values shown in Table 10, would seem to be of special significance in suggesting that breaking-strength determinations may be even a better measure of tendency to lodge than is lodging itself.

This anomaly is of course easily explained by the fact that differences in lodging between varieties in any particular season are closely related to the stage of growth at which weather favorable to lodging occurs, and that an accurate evaluation of varieties with regard to lodging tendencies requires numerous observations extending over many years, while these same limitations possibly do not apply, or at least do not apply to a like degree, to breaking-strength determinations. It is also pertinent to note that estimates of lodging are subject to unusually large errors of personal judgment, partly because of the need of taking into consideration the degree of lodging as well as the amount. Breaking-strength determinations, of course, are almost entirely impersonal.

No critical studies have been made to determine the reason for differences in breaking strength of the straw. That it is to a considerable extent dependent on stand and probably on the size of the culm is rather clearly shown by the partial correlations of Table 8. The high interannual correlations of Table 10 indicate that whatever may be the factors that cause these differences, they are inherited or related to heritable factors. If differences in size due to stand should be found to be a principal factor, the relation could be explained by the well-known tendency of soft wheats to tiller less than hard wheats.

It seems reasonable to conclude that while the data leave much to be desired there can be little doubt as to a relation between lodging and breaking strength and that some method of determining breaking strength such as proposed here may be very useful in developing new varieties resistant to lodging.

SUMMARY

An instrument is described for use in determining the breaking strength of straw under carefully controlled conditions. This instrument was utilized to test the breaking strength of wheat straw of different varieties grown in field plots and in the cereal crop nursery at Manhattan, Kans. In general it was observed that the straw of

soft wheats which show resistance to lodging was more difficult to break than that of hard wheats which lodge easily; the straw of varieties intermediate as to their tendency to lodge occupied an intermediate position with respect to breaking strength. Correlations between lodging in various seasons were not statistically significant, but those between the breaking strength of straw in different seasons were both high and highly significant. This anomaly is explained by the fact that the percentage of lodging is governed by weather conditions, the stage of growth, and variations in individual estimates to a much greater extent than is breaking-strength determinations. It is suggested that the instrument described may be useful in helping to select new wheat varieties to lodging by effecting accurate measurements of the breaking strength of their straw.

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CHARACTERISTICS ASSOCIATED WITH ABORTION AND INTERSEXUAL FLOWERS IN THE EGGPLANT[1]

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INTRODUCTION

The structures and processes concerned in flower and fruit formation in the eggplant have received very little consideration. The abortion and dropping of excessive numbers of flowers often take place, and under certain sets of conditions they may result in a very poor set of fruit. The conditions causing these abnormalities and the altered structures of the reproductive organs are relatively little known.

A study of the interrelationship of the size of flower clusters, diameter of the pedicels in the inflorescence, length of the style and anthers, development of the ovule and embryo sac, the phloem area of the pedicels, and the percentage of fruit setting was made in an effort to learn more about the characters concerned in fruit setting of the eggplant.

In these investigations the writer has confined his attention to the study of (1) flower production and flower abortion throughout the season in relation to the temperature; (2) the relation of the number of aborting flowers and buds to the size of inflorescence; (3) a comparison of the length of styles of developing and aborting flowers; (4) the relation of diameter of the pedicel to the lengths of style and anthers borne on these pedicels; (5) the relation between the amount of phloem area in the two pedicels of 2-flowered inflorescences; (6) the relation between the length of style and the degree of degeneration of the ovules and embryo sacs; and (7) a varietal comparison of flower production, abortion, and style development.

MATERIAL AND METHODS

The Black Beauty variety was used in all the experiments. The plants were grown in the gardens of the Department of Horticulture at the Oklahoma Agricultural Experiment Station. The seed was sown in flats in the greenhouse, shifted to pots in the usual manner, and transplanted to the gardens May 1, 1930. Flower production, abortion, and style development data were obtained from eight varieties of eggplant grown during 1930 in the gardens of the Vegetable Crops Department, Cornell University.

[1] Received for publication Feb. 4, 1931; issued July, 1931. The major portion of the data contained in this paper was taken at the Oklahoma Agricultural Experiment Station; the remaining data were obtained from a variety planting belonging to the Vegetable Crops Department at Cornell University. Through the courtesy of Prof. Paul Work, of the vegetable crops department, eight varieties of eggplant were made available to the writer for study. The writer is indebted to H. L. Cochran, a senior student in the Vegetable Crops Department at Oklahoma Agricultural and Mechanical College, for the data in Tables 1 and 2.

EXPERIMENTAL WORK

ANTHESIS AND BLOSSOM DROP

Ten plants of approximately equal size and stage of development were selected and a complete daily record of all flowers opening and of those dropping was kept separately for each plant.

TABLE 1.—*Rate of eggplant anthesis in 1930*

Date	Number of flowers opening on plant No.—										Total	Average
	1	2	3	4	5	6	7	8	9	10		
June 7							1				1	0.1
June 8						1					1	.1
June 9												
June 10	1			1							2	.2
June 11					1						1	.1
June 12												
June 13	3	1	1								5	.5
June 14						1					1	.1
June 15								2			2	.2
June 16												
June 17		1			1						2	.2
June 18					2	1	1	1			5	.5
June 19							2				2	.2
June 20					4	1	1				6	.6
June 21		1	4		1	2	2		2	1	13	1.3
June 22				1					3		4	.4
June 23	3	6	3	5	1	2	1	2	1	5	29	2.9
June 24				2	1	3			1	1	8	.8
June 25	1	2	1			1		2	1	1	9	.9
June 26	1		1	3	1	3		2		1	12	1.2
June 27	4		1	1	1	3		3		1	14	1.4
June 28			1					2			3	.3
June 29	2	1			3	1	2	6	2		17	1.7
June 30			2	2	3		3	2	3	3	18	1.8
July 1								1	2		3	.3
July 2			1				2	1			4	.4
July 3		1								2	3	.3
July 4												
July 5	2					1		2	1		6	.6
July 6	1								1	1	3	.3
July 7										1	1	.1
July 8												
July 9	1			1		1		1	2	4	10	1.0
July 10	1							1			2	.2
July 11	3							2			5	.5
July 12												
July 13					1						1	.1
July 14												
July 15												
July 16			1								1	.1
July 17												
July 18												
July 19												
July 20 *												
Total	23	13	16	16	20	21	15	30	19	21	194	

* Record taking was discontinued after July 20, as no flowers had opened since July 16.

Table 1 gives the number of flowers opening each day on the different plants from June 7 to July 20. No definite flowering peaks are shown, although most of the flowering occurred during the last 10 days in June, with very sparse flowering thereafter. With a few exceptions the amount of flowering appears to have been influenced but little by the temperature, although for the entire period there is a correlation coefficient of 0.41. The influence of temperature is more noticeable during the first than during the last part of the flowering period. In Figure 1 the amount of flowering and blossom dropping is plotted along with the mean daily temperature for the same period.

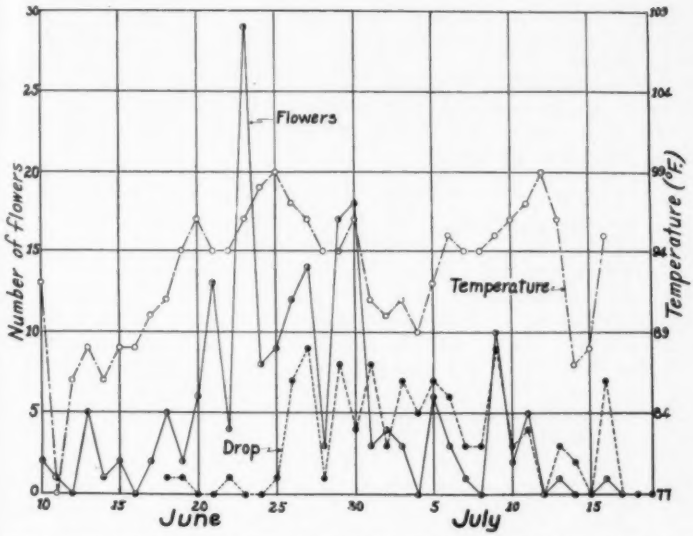


FIGURE 1.—Data for opening and dropping of flowers (average for all plants) as correlated with mean temperatures

TABLE 2.—*Rate of blossom dropping from eggplants in 1930*

Date	Number of flowers dropping from plant No.—										Total	Average
	1	2	3	4	5	6	7	8	9	10		
June 18	1										1	0.1
June 19		1									1	.1
June 20												
June 21												
June 22					1						1	.1
June 23												
June 24												
June 25										1	1	.1
June 26	1				2	1			2	1	7	.7
June 27		1	1		1	3	1		2		9	.9
June 28				1							1	.1
June 29	1	1		2	1	1		1		1	8	.8
June 30	1	1		1		1					4	.4
July 1		2	1	1	2			2			8	.8
July 2	1			1	1						3	.3
July 3	1		1		1	2	1		1		7	.7
July 4					2	2		1			5	.5
July 5				1		1	3			2	7	.7
July 6	1	1						2	1	1	6	.6
July 7							2	1			3	.3
July 8	2							1			3	.3
July 9						1	2	3	3		9	.9
July 10	1					1				1	3	.3
July 11	1			1				1		1	4	.4
July 12												
July 13								2		1	3	.3
July 14	1									1	2	.2
July 15												
July 16					1			3	2	1	7	.7
July 17												
July 18												
July 19												
July 20 [a]												
Total	12	7	3	8	12	13	9	17	11	11	103	

[a] Record taking was discontinued after July 20, as no flowers had dropped since July 16.

Table 2 and Figure 1 give the number of flowers dropping each day from the different plants from June 18 to July 20. In general, the flower-dropping curve parallels the flowering curve. The dropping of flowers apparently is influenced but little by the temperature. Other data show that because of the poor structure of some of the flowers, fruit setting is inhibited and flower dropping follows, regardless of the temperature.

FLOWER PRODUCTION, ABORTION, AND STYLE DEVELOPMENT

Twenty-five plants of approximately equal stage of development were selected, tagged, and the following data obtained from each plant throughout the season: (1) Number of flowers and buds per plant; (2) number of inflorescences per plant; (3) number of flowers per inflorescence; (4) number of fruits setting; (5) total number of aborted flowers and buds; (6) number of aborted flowers of 1, 2, 3, 4, and 5 flowered inflorescences; (7) number of buds aborted; (8) number of aborted flowers with poorly developed styles; and (9) number of aborted flowers with well developed styles. These data are presented in Table 3.

TABLE 3.—*Flower production, abortion, and style development in the egg plant*

Plant No.	Number of flowers and buds per plant	Number of clusters per plant	Number of flowers per cluster	Number of fruits setting	Number of aborted flowers and buds	Number of aborted flowers in—[a]					Number of flowers unopened when aborted	Number of aborted flowers with—	
						1-flowered inflorescenses	2-flowered inflorescenses	3-flowered inflorescenses	4-flowered inflorescenses	5-flowered inflorescenses		Poorly developed styles	Well developed styles
1	19	10	1.9	7	12		[2]^3 (6)	[2]^3 (6)			2	10	
2	24	12	2.0	10	14	1	[2]^2 [1]^3 (7)	[2]^3 (6)			3	10	1
3	20	10	2.0	3	17		[2]^3 [1]^2 (8)	[3]^2 (6)	3		1	16	
4	19	13	1.5	10	9	1	[2]^2 [1]^2 (6)	[2] (2)			1	7	1
5	14	13	1.1	8	6		[2] [1]^2 (4)	[2] (2)				5	1
6	8	3	2.7	2	6		[2] (2)	[2]^2 (4)				6	
7	29	15	1.9	12	17		[2] [1]^7 (9)	[2]^2 (4)	4		1	15	1
8	20	10	2.0	8	12		[2]^2 [1] (5)	[3] [2]^2 (7)			3	9	
9	10	5	2.0	4	6		[2] [1] (3)		3			6	
10	10	5	2.0	4	6		[2] [1] (3)		3		2	4	
11	16	9	1.8	7	9	1	[2]^2 (4)	[2]^2 (4)			2	7	
12	29	12	2.4	10	19		[2] (2)	[2]^7 (14)	3		12	7	
13	7	5	1.4	4	3			[3] (3)				3	
14	17	7	2.4	8	9		[1]^1 (4)	[2]^2 [1] (5)			2	7	
15	20	8	2.5	7	13		[2]^2 [1]^3 (7)	[2] [1] (3)	3		1	12	
16	19	10	1.9	9	10		[2] [1]^2 (4)	[2]^3 (6)			3	7	
17	10	5	2.0	4	6		[2] [1] (3)		3		3	3	
18	12	6	2.0	4	8		[2]^2 [1] (5)		3		2	6	
19	17	8	2.1	6	11		[2] [1]^3 (5)	[3] (3)	3			11	
20	16	7	2.3	7	9		[1]^3 (3)	[3] [2] [1] (6)			5	4	
21	27	14	1.9	12	15		[2] [1]^3 (5)	[2]^2 [3] (7)	3		5	10	
22	36	17	2.1	12	24		[2]^3 [1]^4 (10)	[2]^3 [3] (9)		5	7	17	
23	31	13	2.4	4	27		[2]^6 (12)	[3]^3 (9)	[3]^2 (6)		7	20	
24	23	10	2.3	7	16		[2]^3 [1]^2 (8)	[2]^4 (8)			6	10	
25	21	11	1.9	11	10		[1]^2 (2)	[2] (2)	[3]^2 (6)		5	5	
Total	474	238	50.5	180	294	3	127	116	43	5	73	2.7	4
Average	18.96	9.52	2.0	7.20	11.76	0.12	5.08	4.64	1.72	.20	2.92	8.68	.16
Per cent						1.0	43.2	39.5	14.6	1.7	24.8	98.2	1.8

[a] The numbers inclosed in brackets designate the number of flowers that have dropped from one inflorescence; the exponent of the number in the bracket designates the number of inflorescences in which this has occurred. The number in parentheses is the total number of flowers that have dropped from that type of inflorescence.

Table 3 shows the number of flowers dropping from each inflorescence in each of the 5 types of clusters. In 40 of the 2-flowered inflorescences both flowers of the inflorescence dropped; in 47 inflorescences only 1 flower dropped from each. In 3 of the 3-flowered inflorescences only 1 flower of each inflorescence dropped; in 40 inflorescences, 2 flowers dropped from each, and in 11 inflorescences all 3 of the flowers dropped. In 13 of the 4-flowered inflorescences 3 flowers dropped from each and in only 1 inflorescence did all of the flowers drop. All 5 flowers dropped from the only 5-flowered inflorescence that occurred on the 25 plants. Only 3 flowers dropped from the 1-flowered inflorescences. Column 12 of Table 3 shows that on an average 2.92 buds dropped per plant, or 24.8 per cent of the total abortions. Columns 13 and 14 classify the aborting flowers as to style length. It appears very significant that of the 221 flowers that dropped 98.2 per cent had poorly developed styles and only 1.8 per cent had styles of normal length. These data on the relative development of the styles of aborting and normal flowers appear even more significant when they are compared with the differences in the diameters of the pedicels of these flowers.

The average number of flowers and buds produced per plant was 18.96; the number of inflorescences per plant was 9.52, the average number of flowers per inflorescence being approximately 2. Bailey (*1, p. 23*) [2] stated that—

> as a rule, egg plant flowers are borne singly, but there is always a distinct joint or elbow in the pedicel which marks the loss of the extra flowers. Occasionally a cultivated plant produces a several-flowered inflorescence, but in such cases only the lowest flower is perfect.

Apparently no further cognizance has been taken of these observations. Thompson (*9*) describes the flowers as being large, violet colored, and borne singly opposite the leaves. Jones and Rosa (*5*) state that "the flowers are generally solitary and are located on the branches opposite the leaves." It is also recorded that the flowers are hermaphroditic.

COMPARISON OF STYLE AND ANTHER LENGTH IN FLOWERS WITH POORLY DEVELOPED AND WELL DEVELOPED PEDICELS

On July 3, 1930, two 2-flowered inflorescences were selected from each of 25 plants. The smallest diameter of the pedicel of each flower and the lengths of the style and anthers were measured and the measurements in each inflorescence kept together. Plate 1, A, shows the relative size of flowers and pedicels of a typical 2-flowered inflorescence. The diameters of the pedicels of the large-pediceled flowers ranged from 3 to 4.5 mm., averaging 3.57 ± 0.035 mm., those of the small-pediceled flowers ranged from 1 to 2 mm., averaging 1.59 ± 0.010 mm. The lengths of styles of the large-pediceled flowers ranged from

[2] Reference is made by number (italic) to Literature Cited, p. 93.

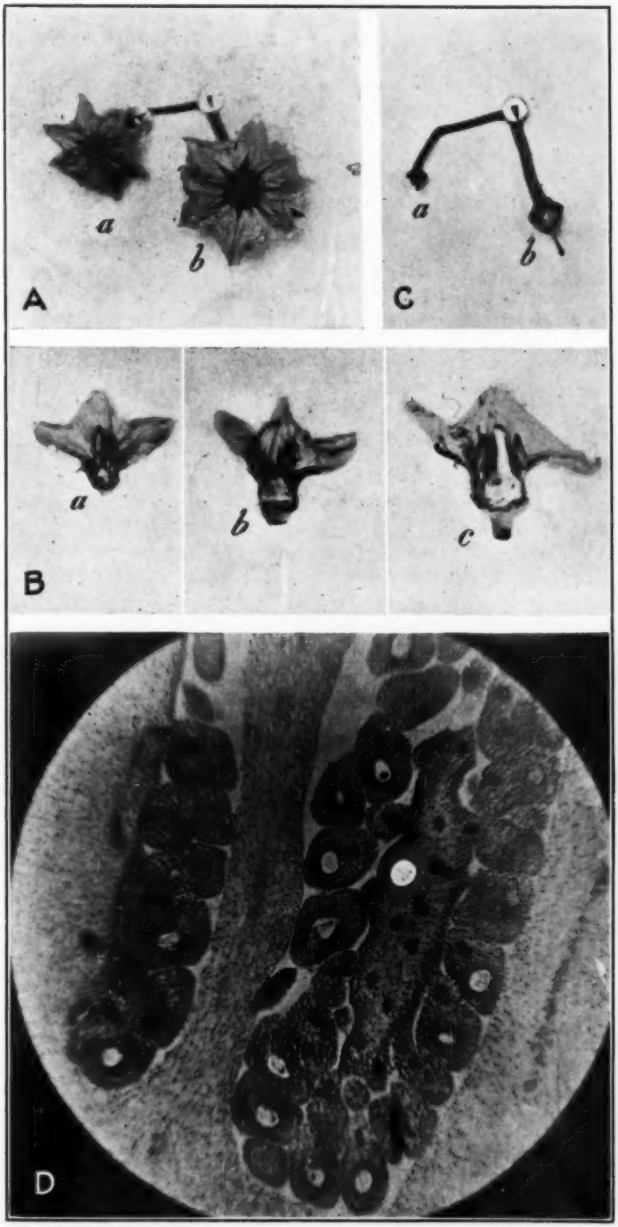
EXPLANATORY LEGEND FOR PLATE 1

A.—Typical 2-flowered inflorescence showing the relative size of the flowers and pedicels. Flower *a* is referred to as flower No. 2, *b* as flower No. 1.

B.—Relative size of ovary and stamens, and length of style of eggplant flowers. Flower *a* was borne on a small pedicel; note the well-developed stamens and extremely small ovary and short style. Flowers *b* and *c* were borne in the same inflorescence, *b* on a small pedicel, *c* on a large pedicel.

C.—Same inflorescence as shown in A, with corolla and stamens removed. Note relative size of pedicels and ovaries and length of style. Flower No. 2 at *a* and No. 1 at *b*.

D.—Section of pistil of a large-pediceled, long-styled flower at time of anthesis.



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7 to 11 mm., averaging 9.32 ± 0.099 mm.; those of the small-pediceled flowers ranged from 0 to 4 mm., averaging 1.88 ± 0.105 mm. However, the range of anther length of the large-pediceled flowers was 6 to 9 mm., with an average of 7.5 ± 0.058 mm.; those of the small-pediceled flowers ranged from 6 to 8 mm., with an average of 7.3 ± 0.052 mm.

Flower No. 1 of each 2-flowered inflorescence had a larger pedicel diameter and several times the length of style of flower No. 2 on the same inflorescence. The average length of the styles borne on the large pedicels was 9.32 ± 0.099 mm.; those borne on the small pedicels averaged only 1.88 ± 0.105 mm.

The anthers, however, did not show any such corresponding decrease in size when borne on small pedicels. The average length of anthers borne on large pedicels was 7.5 ± 0.058 mm., and those borne on small pedicels was 7.3 ± 0.052 mm. Plate 1, B, shows the comparative size of male and female organs of flowers on large and small pedicels in the same inflorescence. The ovary and style of the small-pediceled flower are greatly stunted, but there is practically no difference in the size of the anthers in the two flowers. Whatever the limiting factor may be, it appears to inhibit greatly the development of the female organs but to alter the male organs only slightly. Pollen from the anthers of short-styled flowers was viable and able to fertilize the eggs of well-developed flowers.

Plate 1, C, shows the relative size of pedicels and ovaries and the length of style of the flowers of 2-flowered inflorescences.

RELATION BETWEEN THE AMOUNT OF PHLOEM AND TOTAL CROSS-SECTIONAL AREA OF PEDICELS OF 2-FLOWERED INFLORESCENCES

For a comparative study of the relative areas occupied by the phloem in each of the pedicels of 2-flower inflorescences, free-hand cross sections at the smallest diameter of the pedicels were made, mounted in water, projected on paper, and the phloem area and total cross section of the pedicel traced. A microprojection apparatus was used. The relative areas of phloem and total pedicel cross section of the two flowers in each inflorescence were then obtained by using a polar planimeter. With a magnification of 60, the cross-sectional area of the large pedicels ranged from 73.29 to 78.65 square inches, with an average of 76.3 ± 0.323 square inches; those of the small pedicels ranged from 10.91 to 12.01 square inches, with an average of 11.26 ± 0.218 square inches. With the same magnification the cross-sectional area of the phloem tissue of the large pedicels ranged from 4.97 to 5.25 square inches, averaging 5.12 ± 0.018 square inches; those of the small pedicels ranged from 0.32 to 0.42 square inches, averaging 0.36 ± 0.007 square inches.

The cross-sectional area of one pedicel is much larger than that of the other in 2-flowered inflorescences. The cross-sectional area of the phloem in the larger pedicel averages 14.2 times that of the phloem in the smaller pedicel, although the total cross-sectional area of the larger pedicel is only 6.8 times that of the smaller one. The ratio of the total cross-sectional area of the pedicel to the phloem cross-sectional area also shows that the amount of this conducting tissue is over twice as great in the large pedicel, in proportion to the total area, as in the smaller pedicel. The stunted style growth of the smaller pediceled flowers is directly related to the small area of the

phloem of these pedicels. It is highly probable that the limited function of these restricted channels for the transference of organic nutrients has an effect upon the growth of the styles. It is very interesting to find, however, that the growth of the male portions of the flowers is scarcely affected by the reduced phloem area.

Numerous investigations on the physiological control of sex in plants show that proper nutrition (due to fertile soil, length of day, soil moisture, position on the plant, etc.) is often directly related to the ratio of sex. Halsted (*4*) states that in hemp grown on heavily manured soil, there was an excess of pistillate plants while in the adjoining unmanured plot there was nearly a 1:1 ratio. Pritchard (*6*) found that it was possible to change the sex by altering the environment. In nearly every instance in which food affected the sex ratio, favorable nutritive conditions tended to produce females and unfavorable conditions produced males. Correns (*2*) found that the hermaphroditic flower of *Silene roemeri* required more nutrients than the staminate flower, and, in poor nutrition, the hermaphroditic flower was produced less abundantly. Schaffner (*7*) has completely reversed the sex in Arisaema, in both directions, by altering the water and plant-food supply. Dryness of the soil caused all the monoecious and most of the pistillate plants to change over to the staminate form. Nearly all of these plants, as well as those originally staminate, became pistillate the following year under the influence of heavy manuring and abundant moisture. Gardner (*3*) concluded that femaleness in plants is associated with rich soils, abundant moisture, liberal spacing, the vigor of youth, and favorable growth conditions in general; maleness is associated with less favorable growth conditions. Schaffner (*8*) later stated that the percentage of reversal and even the very possibility of reversal depends to a considerable extent on whether the plant is drawing the proper nutrients, especially nitrogen, from the substratum at the time. The reversal of sex is probably brought about by a physiological condition dependent in some way on the carbohydrate-nitrogen ratio in the cells.

The plants of these experiments were poorly nourished. No fertilizer was added to the soil at any time during the growing season and the condition of the plants indicated a shortage of nitrogen. The soil moisture was also a very important limiting factor. Only 1.89 inches of rain fell during the entire growth period. A small surface irrigation was given on July 3, although it did not increase the soil moisture very greatly.

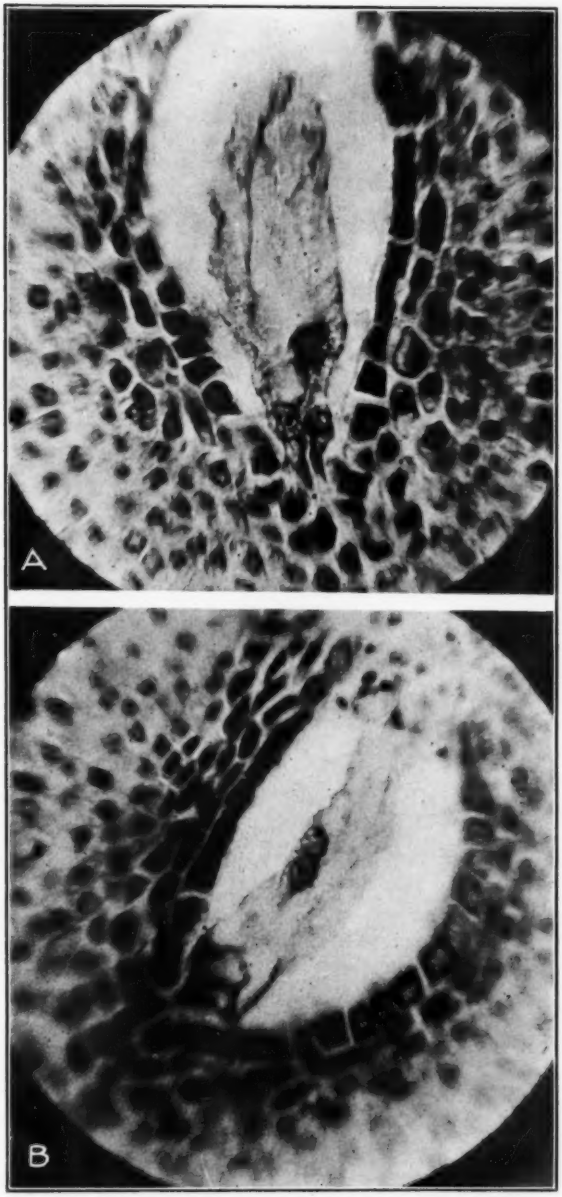
RELATION BETWEEN THE LENGTH OF STYLE AND THE DEGREE OF DEGENERATION OF OVULES

From the observations mentioned above it is evident that the diameter of the pedicel of flower No. 2 is smaller than that of the pedicel of flower No. 1 in the same 2-flowered inflorescence and also that the style length of flower No. 2 is always shorter than that of

EXPLANATORY LEGEND FOR PLATE 2

A.—Section of ovule of long-styled flower at anthesis, showing embryo sac with two synergids and the egg cell. Compare with Plate 3, A.

B.—Section of ovule of long-styled flower at anthesis showing well-developed cells of nucellus and inner integument and embryo sac with two polar nuclei fusing just previous to fertilization. Compare with Plate 3, B.



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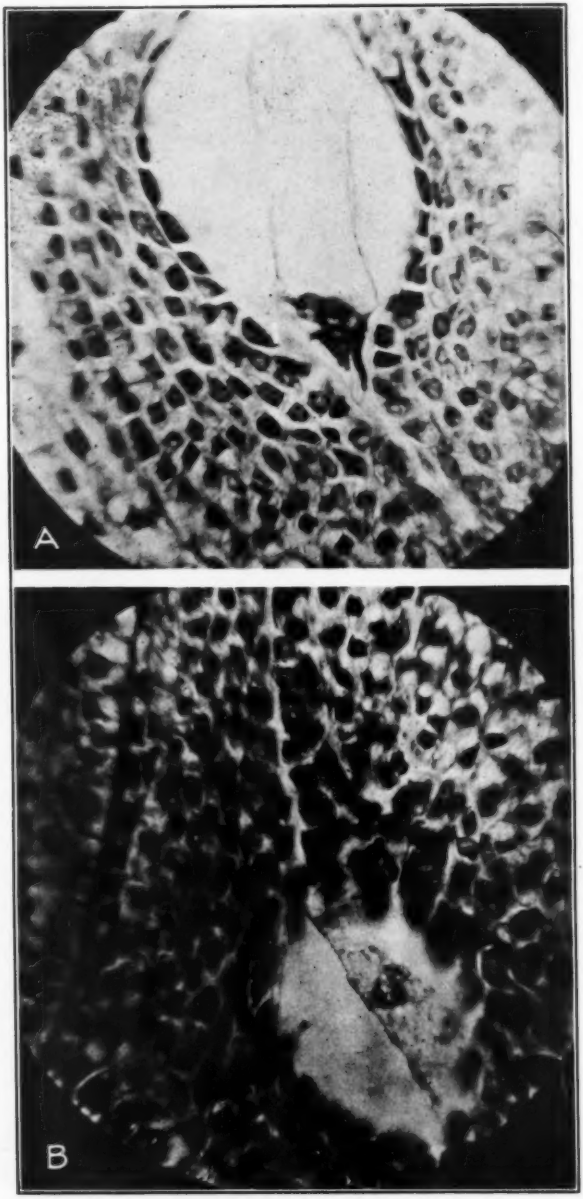

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flower No. 1. It is interesting to know what relation, if any, the stunted styles have with the development of the ovules and at what stage in their development the differences may appear. Pistils of 2-flowered inflorescences, in which both flowers had opened on the same day, were selected on the date of anthesis. The material was killed in Karpechenko's solution, fixed, dehydrated, and embedded in paraffin according to the usual procedure. The sections were stained in Haidenhain's haematoxylin.

Plate 1, D, shows the arrangement and stage of development of a group of ovules of the large-pediceled flowers at the time of anthesis. The ovules are very numerous, completely covering the free surface of the placenta. Plate 2, A and B, shows two stages of development of the embryo sacs of large-pediceled normal-styled flowers. The integument is very thick, the edges not actually joining over the end of the embryo sac, however, so that there remains a narrow channel, the micropyle, through which the pollen tube may enter. Plate 2, A, shows the embryo sac with two synergids in view and what appears to be the egg cell.

Plate 2, B, shows the embryo sac with two polar nuclei fusing just previous to fertilization. Plate 3, A and B, shows two different stages of development of small-pediceled short-styled flowers at the same stage as those in Plate 2. The cells of the nucellus and inner integument of Plate 3, A, appear to be partially degenerated. The cells are smaller, flatter, and less densely stained. Comparisons of embryo-sac development in pistils borne on large pedicels with those on small pedicels show practically no differences in their development. Although slight differences were noted, there appears to be no marked parallelism between the stuntedness of styles and the degree of degeneration of the ovules and embryo sacs. Nunerous hand pollinations of short-styled flowers resulted in about 50 per cent set of fruit, while those not pollinated artificially very rarely set fruit. This also tends to support the view that at least up to the time of anthesis the ovules and embryo sacs of short-styled flowers are developed normally.

VARIETAL COMPARISON OF FLOWER PRODUCTION, ABORTION, AND STYLE DEVELOPMENT

During the late summer and fall of 1930, data were obtained from eight varieties of eggplant at Ithaca, N. Y. Among these was Black Beauty. As this variety had been grown at Oklahoma it was possible to compare its behavior under different environmental conditions. These results are presented in Table 4.

EXPLANATORY LEGEND FOR PLATE 3

A.—Section of ovule of short-styled flower showing partially degenerated cells of the nucellus and inner integument. Compare with Plate 2, A.

B.—Section of ovule of short-styled flower at anthesis showing embryo sac containing one cell. Compare with Plate 2 ,B.

TABLE 4.—*Varietal comparisons of flower production, abortion and style development in eggplants*

[Data taken from 10 plants of each variety]

Variety	Number of flowers and buds	Number of clusters	Number of flowers per cluster	Number of fruits setting	Aborted flowers and buds	
					Number	Per cent
Early Long Purple	38	37	1.02	36	2	5.3
California Tree	30	28	1.07	28	2	6.7
Florida Special	42	31	1.35	32	10	23.8
Manatee Special	38	31	1.22	31	7	18.4
Florida Highbush	32	22	1.45	18	14	43.7
Extra Early Dwarf Purple	71	70	1.01	61	10	14.1
New York Improved	106	67	1.58	71	35	33.0
Black Beauty	175	93	1.88	97	78	44.6

Variety	Aborted flowers in —[a]				Aborted flowers with short styles	
	1-flowered inflorescenses	2-flowered inflorescenses	3-flowered inflorescenses	4-flowered inflorescenses	Number	Per cent
Early Long Purple	1	[1] (1)			2	100
California Tree		[1] ^{2} (2)			2	100
Florida Special		[1] ^{5} (5)	[3] [2] (5)		10	100
Manatee Special	1	[1] ^{6} (6)			7	100
Florida Highbush	1	[1] ^{6} [2] ^{2} (10)	[3] (3)		14	100
Extra Early Dwarf Purple	10				10	100
New York Improved		[1] ^{25} (25)	[2] ^{5} (10)		30	85.7
Black Beauty		[1] ^{33} [2] ^{2} (37)	[1] ^{3} [2] ^{15} [3] (36)	[2] [3] (5)	78	100

[a] The number inclosed in brackets designates the number of flowers that have dropped from one inflorescence; the exponent of the number in the bracket designates the number of inflorescences in which this has occurred. The number in parentheses is the total number of flowers that have dropped from that type of inflorescence.

Inflorescences of more than one flower are very rare in the Extra Early Dwarf Purple, Early Long Purple, and California Tree varieties. These three varieties also had a very small number of aborting flowers. With the exception of those of Extra Early Dwarf Purple practically no flowers in any of the eight varieties aborted in a single-flowered inflorescence. The Black Beauty variety averaged 1.88 flowers per cluster, which was the highest number for the eight varieties but was slightly lower than that for the same variety grown in Oklahoma.

In general, those varieties having the greatest number of flowers per cluster also had the greatest percentage of aborted flowers. In all varieties, except the New York Improved, all of the aborted flowers had poorly developed styles. Eighty-eight and six-tenths per cent of all aborted flowers were borne in 2 and 3 flowered inflorescences. Of the total number of dropped flowers and buds in the Black Beauty variety 47.4 per cent dropped from inflorescenes of 2 flowers, 46.2 per cent from clusters of 3, and 6.4 per cent from clusters of 4 flowers.

SUMMARY

Eggplants under observation at Stillwater, Okla., reached a flowering peak during the last 10 days in June. Some of the variations in the amount of flowering appear to have been due to fluctuations in temperature. In general, the amount of flower dropping parallels

the amount of flowering and apparently is influenced but little by the temperature.

Flowers are rarely borne singly in the Black Beauty variety of eggplant. Two hundred and thirty-eight inflorescences averaged 2 flowers each, ranging from 1 to 5 per inflorescence.

Under field conditions, with 474 flowers and buds under observation, 62 per cent of them dropped from the inflorescence. Of the total number of dropped flowers only 1 per cent dropped from inflorescences of 1 flower; over 82 per cent came from inflorescences of 2 and 3 flowers. Ninety-eight and two-tenths per cent of the flowers that dropped had short, poorly developed styles. Practically all of the flowers that dropped were borne in multiflowered inflorescences and had very small pedicels.

As a group the diameters of the pedicels are directly related to the lengths of the styles borne on these pedicels. The sizes of the anthers, however, do not appear to be influenced by the diameter of the pedicels on which they are borne.

The amount of phloem cross-sectional area in the larger pedicel of 2-flowered inflorescences is much greater in proportion to the total pedicel cross-sectional area than it is in the smaller pedicel. There is a direct relation between the small size of pedicel, small phloem area in the pedicel, and the weak expression of femaleness in the flowers on this pedicel. This type of flower is designated flower No. 2 in 2-flowered inflorescences. (Pl. 1, C.) The literature on sex expression shows a generally prevailing opinion that weak femaleness in flowers is strongly associated with unfavorable conditions of growth and nutrition.

Histological studies of short-styled and normal-styled flowers at the time of anthesis failed to show any marked parallelism between the stuntedness of styles and the degree of degeneration of ovules and embryo sacs.

In a study with eight varieties of eggplants at Ithaca, N. Y., it was found that some varieties rarely bear more than one flower in an inflorescence. These same varieties also have a small percentage of aborting flowers. The habits of flower production, abortion, and style development of the Black Beauty variety grown at Ithaca, N. Y., were similar to those of the same variety grown in Oklahoma.

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